Faunal Community Structure Associated with the Bed of Subtropical Brown Seaweed *Sargassum siliquastrum* (Turn.) Ag. in Hong Kong Eastern Waters, HKSAR

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A Thesis Submitted in Partial Fulfillment of the Requirement for the Degree of Master of Philosophy in Biology

The Chinese University of Hong Kong

November 2009

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Taylor for their valuable comments and suggestions on this thesis.

I would also like to express my gratefulness to Mr. Y.H. Yung for taking me safe to and from the field sites and sharing his experience in maritime affairs. Special acknowledgements are also given to Mr. Ben H.B. Yeung and Mr. Ng for his technical support and advice.

Special thanks are made to my remarkable buddy Mr F.F. Yeung for his assistance in the field and my helpful labmates Mr. Frank C.C. Cheang, Ms. Sam M.W. Lee, Ms. Winnie S.Y. Wong, Mr Anton Y.T. Tsang, Mr Chris H. L. Fung, Mr Atwood Y.M. Chiu, Ms. Y.H. Lam and Ms. Y.M. Tsang for their suggestions on my project and cheers on the completion of this thesis. I am very much delighted to work and dive with them in Hong Kong and in other places around the world. The times and the friendships are always cheerful and unforgettable. I would treasure every breath, every photo and every moment I took with my beloved ones.

I would like to express my deepest love to my parents and brother who nourish me with their care and understanding to let me do what I want. Sincere appreciations are also given to my friends Ms. Rita L.M. Liu, Ms. Christy Y.H. Ng, Ms. W.N. To, Ms.

Aeri N.Y. Ng, Ms. Vanessa W.S. Chan, Ms. Fandy S.F. Lee, Ms. Elsa Y.Y. Lee, Mr. Klinsmann K.L. Cheung, Mr. Tony H.T. Sung and Mr. Johnson Y.F. Cheung and my fellowship for their endless encouragements in my hard times and for sharing the happiness. Lastly, I should be grateful if this study work could contribute to the appreciation and conservation of our nature, and I sincerely hope to work for the environment in the rest of my enjoyable life.

Abstract

Seaweeds have been extensively cultivated or harvested from the wild for their high economic values. Unsustainable harvesting could result in denudation of the seaweed bed and shifts in the community structure from a macroalgae-dominated to one with barren grounds, and ultimately with irrecoverable trophic cascade. Seaweed bed is believed to act as a sanctuary for economically important marine resources. However, the functional role of seaweed ecosystem is often overlooked when compared with the other marine ecosystems, e.g. coral reef. It is therefore of utmost importance to fill in the knowledge gap on the habitat role of seaweed beds, especially for those in subtropical region like Hong Kong, by generating baseline information on the faunal assemblage composition associated with the seaweed beds.

The faunal assemblage, including zooplankton and epiphytic fauna, associated with the extensive bed of *Sargassum siliquastrum* in Hong Kong eastern waters and its temporal change from November 2006 to January 2008 were examined. In Lung Lun Tsui (LLT) at Tung Ping Chau Marine Park (TPCMP) and Lo Fu Ngam (LFN) in Sai Kung, a total of 72 species and/or taxonomic groups of zooplankton were recorded throughout the sampling period. Zooplankton abundance and species richness were relatively higher from January to March, September and November 2007, which was

likely brought about by the prevailing monsoons and discharge from the Pearl River. Besides, the relationships between faunal structure and the *Sargassum siliquastrum* phenology (i.e. growth stages: slow growth from March to August; rapid growth from September to November; reproductive stage from December to January; and die-back stage from January to February), the seaweed structural complexities, as well as environmental parameters within the seaweed beds were verified. Zooplankton assemblage structure, especially in terms of its species richness, in the *Sargassum siliquastrum* bed was more distinctly different from that in the unvegetated habitat particularly during the rapid growth, reproductive and dieback stages of *Sargassum siliquastrum*. Zooplankton species richness was more influenced by seaweed phenology, as indicated by seaweed length, than by the physical environmental factors. The close association between zooplankton assemblage and seaweed phenology was likely due primarily to the substantial supply of food sources by the seaweeds during periods of seaweed reproduction and dieback, and the complex structure offered by the vegetation, in particular the dense canopy, during the rapid growth, reproductive and dieback stages of the seaweed.

The effects of canopy removal on zooplankton abundance and species diversity were investigated by comparing the zooplankton assemblage in treatment (i.e. canopy

elimination), control (i.e. canopy intact) and unvegetated environment. Removal of the seaweed canopy resulted in a more significant impact on zooplankton species richness than on its abundance. With zooplankton species richness in treatment and unvegetated habitats becoming statistically similar after canopy removal, the role of seaweed canopy in structuring the zooplankton species diversity in vegetated habitats was evident.

The epiphytic faunal community associated with the seaweed bed of *Sargassum siliquastrum* and its temporal variation with seaweed phenology were also investigated in this study. Through the whole course of sampling, a total of 163 species (including morpho-species) and taxonomic groups of epiphytic organisms on *Sargassum siliquastrum* were identified in three sites LLT, LLS (Lung Lok Shui) in TPCMP and LFN in Hong Kong eastern waters. The peak in total faunal abundance and species richness in late winter and early spring (Apr07, May07 and Feb08) was due to the seasonal flux of some common taxon groups. This flux was likely supported by the seasonal burst of food items, together with a lower level of anti-herbivory and anti-fouling defense in the form of lower levels of secondary metabolites, during the reproductive and dieback stages of *Sargassum siliquastrum*. *Sargassum siliquastrum* bed was shown to function as a site for larval settlement and

recruitment of epiphytic faunal species, particularly during the rapid growth, reproductive and dieback stages of the seaweed. Synchronization of faunal life cycles, e.g. reproductive period, with phenology of *Sargassum siliquastrum* was illustrated. In addition, *Sargassum siliquastrum* bed acted as nursery and nesting grounds for ecologically and economically important fishery species, notably mantis shrimp, lobster and common rockfish. The essence of seaweed bed as a nursery habitat was also evident even during the slow growth stage of *Sargassum siliquastrum.* Environmental factors, namely temperature, dissolved oxygen and salinity levels, were unlikely to exert an immediate effect on the epiphytic faunal assemblage.

The connection between epiphytic faunal assemblage structure with physical properties, such as length, branch number and biomass, of *Sargassum siliquastrum* was investigated. The within-plant faunal zonation of *Sargassum siliquastrum* was also exhibited in this study. The increase in the physical properties of *Sargassum siliquastrum* generally produced concomitant increase in the abundance and diversity of the associated faunal community. The macroalgal biomass, expressed as fresh weight, provided greater effects on epiphytic faunal abundance and species richness, particularly during seaweed reproductive and dieback stages, when compared with other components of structural complexity. The provision of affluent food sources,

enhanced surface area for attachment and protection, as well as amelioration of the strong hydrodynamics, were probably factors that led to the augmentation of faunal numbers and species diversity by an increase in seaweed biomass. Within-plant zonation pattern was more pronounced in seaweed reproductive and dieback stages. Species richness and abundance were, in the main, highest in the lower zone of the algae, including the holdfast.

In this study, the role of the extensive beds of *Sargassum siiliquastrum* as a nursery and nesting ground for zooplankton as well as epiphytic faunal species of economic and ecological significance was highlighted. Above all, the canopy of *Sargassum siliquastrum* was found to serve as a site for larval retention and as larval nursery grounds. Therefore, the conservation values of these seaweed beds should not be underestimated. A strategy to assess environmental impacts caused by coastal developments, which are the major threats to the coastal seaweed communities, as well as the harvesting of seaweed canopy should be put in place to ensure that the complex association between seaweeds and the associated faunal assemblages is sustained for the future.

論文摘要

由於豐富的經濟價值，海藻從古至今被廣泛地培育或在野外收割。無法持續的野外海藻收割可徹底夷平海藻族群，導致生態系統的轉移，甚至造成不能復原的食性層崩塌。雖然海藻床被認爲是具經濟及生態價值海洋資源的庇護所，但海藻床的生境角色相對於其他的生態系統，如珊瑚礁，卻經常被忽略。爲了增加對香港海洋環境的認識、策劃海岸工程對海岸生態影響的評估、設計可持續發展的野外海藻收割措施，填補海藻床在生態系統作用上的知識空白是必需的。

在 2006 年 11 月至 2008 年 1 月期間，我們在香港東面水域進行了對裂葉馬尾藻 (*Sargassum siliquastrum*) 床的組合動物群落，包括附生生物及浮游生物的分析及時間變化的紀錄。在位於東平洲海岸公園的龍鱗咀及西貢的老虎岩，我們在裂葉馬尾藻床內發現 72 物種/分類種的浮游生物。在 2007 年 1 月至 3 月、9 月和 11 月期間，浮游生物的總數及物種多樣性較其他時期爲高，這可能是季候風及珠江流注帶來的影響。另外，浮游生物群落與裂葉馬尾藻物候學 [即生長階段: 3 月至 8 月的新生期 (緩慢生長期)、9 月至 11 月的活躍生長期、12 月至 1 月的繁殖期及 1 月至 2 月的老化期 (回枯期)]、裂葉馬尾藻結構複雜性和環境物理參數的關係亦被查證。結果顯示，在裂葉馬尾藻床和沒有裂葉馬尾藻生境中的浮游生物群落結構，特別是物種多樣性，有著明顯的不同；這現象尤其在裂葉馬尾藻的活躍生長期、繁殖期及老化期 (回枯期)更爲明顯。相比環境物理參數，裂葉馬

尾藻的物候學對浮游生物群落的物種多樣性影響更爲深遠。裂葉馬尾藻的物候學與浮游生物群落結構有著密切的關係，主要是因爲裂葉馬尾藻能提供大量的食物，尤其在裂葉馬尾藻的繁殖期及老化期；另外，茂密的裂葉馬尾藻冠層爲生物提供足夠的空間逃避捕食者。

我們透過比較在實驗組別 (除去裂葉馬尾藻冠層)、對照組別 (保留裂葉馬尾藻冠層) 及沒有裂葉馬尾藻的浮游生物群落，展示除去裂葉馬尾藻冠層對浮游生物群落的數量及物種多樣性引致的影響。結果顯示，實驗組別與沒有裂葉馬尾藻生境的樣品在統計上相似，意味著除去裂葉馬尾藻冠層給浮游生物群落帶來破壞性的效果，特別是物種多樣性。本實驗展示裂葉馬尾藻冠層在組織浮游生物群落重要且顯然的角色。

在位於東平洲海岸公園的龍落水和龍鱗咀及西貢的老虎岩，我們進行裂葉馬尾藻床的附生生物群落結構及其時間變化的調查中發現 163 物種/分類種的附生生物。附生生物群落總數與物種多樣性紀錄在冬末及初春 (07 年 4 月、5 月和 08 年 2 月) 爲最高，這可能是因爲季節性泛起的食物源及裂葉馬尾藻繁殖和老化期期間體內抗草食性化學物的下降，引致常見的附生生物種群季節性的湧入與總數的激增。是次調查顯示，不同生長階段的裂葉馬尾藻床於孕育具經濟及生態價值的附生生物均發揮重要的功能，此作用在裂葉馬尾藻的活躍生長期、繁殖期及老

化期尤其明顯。另外，組合附生生物的生活週期，如繁殖期，與裂葉馬尾藻生長階段表現同步化。我們亦測定環境物理參數對附生生物群落的影響，結果顯示，環境因素，如水溫、溶氧量和鹽度，爲附生生物群落沒有帶來即時的影響。

我們對附生生物群落結構與裂葉馬尾藻物理參數的關係進行調查。結果顯示，裂葉馬尾藻物理參數的提升帶來附生生物群落總數及物種多樣性附隨的增加。在裂葉馬尾藻的物理參數中，馬尾藻生物量比其他物理參數，如長度和枝條數量，對於附生生物群落總數及物種多樣性所起的影響更爲深刻。裂葉馬尾藻生物量的增加替附生生物群落帶來富裕的食物源、增大表面用作附著及保護的面積和流體力學的減緩，產生一個優化的生境供給更多數量及物種的附生生物棲息。此外，我們亦紀錄裂葉馬尾藻個體範圍的成帶現象。紀錄顯示，個體範圍的成帶現象在裂葉馬尾藻的繁殖期及老化期最爲明顯；最高的附生生物總數及物種多種性均紀錄於馬尾藻個體的下層，包括其固著器。

本研究項目顯示廣闊的裂葉馬尾藻床可爲具經濟及生態價值的浮游物種與附生生物提供滋生地及育幼處，強調裂葉馬尾藻冠層於孕育海洋資源幼體，如糠蝦、龍蝦、魚及烏賊等，所擔當的重要角色。因此，海藻床的保育價值是不容忽視的。是次研究所得的數據，均是發展香港近岸藻床保育及管理計劃時所需的重要基本資料。

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Chapter 1

General Introduction

1.1 Seaweeds as Beneficial Resources to Humans

Seaweed resources have long been used as food, medicine, animal feed and natural fertilizers. More recently, they are raw materials for biopharmaceutical products and industrial colloids, and are used as nutrient sequester in aquaculture. Among thousands of seaweed species, *Sargassum* spp., *Turbinaria* spp., *Ulva* spp., *Caulerpa* spp. are sources of vitamins and minerals such as iodine (Indergaard and Minsaas 1991) and are traditionally consumed by the Chinese (Diaz-Piferrer 1979, Baker 1984). The production of iodine-rich powder from *Ecklonia maxima* can help prevent brain damage and mental retardation (WHO 1996). Temperate species of *Porphyra* (nori), *Undaria* (wakame) and *Laminaria* (kombu) are popularly eaten in Japan, Korea and China. In Thailand, *Caulerpa, Ulva* and *Sargassum* are collected for use as salads (Phang 2006). In the Southeast Asian region, Indonesia is the largest consumer and producer of seaweeds through harvesting of wild stocks (FAO 2006). Sixty-one species from 27 genera of seaweeds are consumed as food while 21 species from 12

genera are used as herbal medicine (Istini *et al.* 1998). In addition, seaweeds are used in the field of animal husbandry as feeds and in agriculture as natural fertilizers (Blunden 1991). Large seaweed species such as *Sargassum* spp., *Kappaphycus* spp., *Gracilaria* spp. and *Ulva* spp. are commercially utilized as components in animal feeds, as sources of carotenoids and as binders (de Guzman 1978, Ragan 1981, Mshigeni 1982). In mariculture, *Hypnea*, *Acanthophora* (Phang 2006) and *Ecklonia maxima* (Troell *et al.* 2006) are utilized as feed for abalone. In agriculture, many genera like *Sargassum, Ulva, Hydroclathrus* and *Kappaphycus* spp. are used as soil conditioners (Chidambaram and Unny 1953, Michanek 1979, Mshigeni 1982) due to the water-retaining properties of their phycocolloid, as well as the presence of plant hormònes, minerals and trace elements contained in these seaweeds (Rotmann *et al.* 2003). Extracts from *Sargassum* spp. are utilized in liquid fertilizers on vegetables and grain crops to enhance their production (Montaño and Tupas 1990).

Moreover, seaweeds have been applied in the pharmaceutical manufacturing and colloid production industries (Indergaard and Ostgaard 1991). Some seaweed species like *Asparagopsis taxiformis* (Fenical *et al.* 1979) are raw materials for biopharmaceutical products as they contain bioactive substances that exhibit antibacterial, antiviral and antifungal properties. In South Africa, the kelp *Ecklonia*

maxima is processed to extract its alginate for use in cosmetics, in horticulture as soil improver, and as feed additives and fresh feed in aquaculture (Rotmann *et al.* 2003). Several seaweed species of *Gracilaria* and *Gelidiella acerosa* are sources of phycocolloids like agar which can be valued at US$132 million annually. Furthermore, *Eucheuma* and *Kappaphycus* are sources of carrageenan valued at US$240 million annually (FAO 2004). In England, the waste product from the commercial manufacture of alginates are shown to be able to sequester cadmium, copper, aluminum and zinc ions from metal plating wastewaters and thus can be applied in the removal of heavy metals in the metal plating and processing industries (Sandlands *et al.* 2003). Therefore, not a single part of the seaweeds would be wasted.

In addition to their industrial applications, algae, and in particular seaweeds have been shown to be efficient biofiltration agents in highly eutrophied waters associated with aquaculture (Schramm 1991, Gao and Mckinley 1994, Buschmann *et al.* 1996). Due to their high biofiltration capabilities, the commercially important seaweeds have been cultured in combinations with fish, shrimp, shellfish, abalone and sea urchin. A 1-ha integrated seabream-shellfish-seaweed farm can produce 25 tonnes of fish, 50 tonnes of bivalves and 30 tonnes fresh weight of seaweeds annually in Israel (Neori *et al.* 2004). In China, large-scale cultivation of *Laminaria japonica* (Fei 2004) and

Gracilaria lemaneiformis (Yang *et al.* 2006) has been applied as nutrient sequesters in connection with scallop cultivation to absorb excess quantities of N, P and CO_2. This produces tremendous amount of O_2, thus assisting in the effective control of eutrophication arising from aquaculture in coastal waters at relatively low costs.

Since seaweeds are so economically important natural resources, their mass cultivation has been concurrently developed and adopted in countries of temperate, sub-tropical as well as tropical regions. At present, there are approximately 200 species of seaweeds used worldwide (Zemke-White and Ohno 1999), of which 10 species or genera are intensively cultivated. In 1999, the world annual production of seaweeds amounted to about 10×10^6 tonnes wet weight, the largest part of which came from culture-based practices (FAO 2001). The top 10 species list of aquaculture production is headed by the kelp *Laminaria japonica* with 4.2×10^6 tonnes, cultivated mainly in China (FAO 2001). About 1500 tonnes of the seaweeds *Enteromorpha* spp. and *Ulva* spp. for use in foods are cultivated in Japan each year (Ohno and Largo 1998). In the Philippines, seaweeds and their products are the third most important fishery export. Production of farmed *Kappaphycus/Eucheuma* spp. reached 58 324 dry metric tonnes in 1995 and was valued at US$44 million dollars (Trono 1999). Therefore, seaweeds can bring promising economic benefit to the community,

generate stable job opportunities and be applied in minimizing environmental impacts, e.g. eutrophication, of industrialized mariculture in both developed and developing countries.

1.2 Seaweed Communities as a Habitat

1.2.1 Reasons for being a Favourable Habitat in the Ocean and the Coastal Region

Macroalgal (seaweed) community is one of the highly productive ecosystems in the natural environment, with maximum productivity at 1.8 kg C m^{-2} yr^{-1} and a maximum chlorophyll content of 3 g m^{-2} ground or illuminated surface. In a seaweed stand, this is achieved with an algal biomass of approximately 10 kg m^{-2} (Lüning 1990). Macroalgae are essential primary producers and thus, the important sources of energy supporting the food webs in coastal and shallow marine benthic ecosystems. They contribute substantial amounts of organic matter to nearshore ecosystems (Lüning 1990). They serve as food for invertebrate grazers (Lubchenco 1978), juvenile fish, and waterfowl in coastal food chains (Raffaelli and Hawkins 1996). In the subtidal environment, crustose coralline algae, being the dominant components of coral reef communities (Stearn *et al.* 1977, Glynn *et al.* 1996, Keats *et al.* 1997), contribute

significantly to organic production in coral reefs. They provide food for herbivores with hardened mouthparts (Steneck and Dethier 1994, Steneck 1997). Besides the host seaweed itself, the epiphytic plants on the seaweeds are also food for grazers like amphipods (Norton and Benson 1983, Bologna and Heck 1999). In turn, amphipods and other invertebrates are consumed by predators such as crabs (Epifanio *et al.* 2003). Macroalgal detritus is also a significant source of nutrients in the food web of coastal marine ecosystems (Hicks 1980, Moreno and Jara 1984, Duggins *et al.* 1989, Mann 2000).

Besides being a source of food, seaweeds are also able to provide refuge for many invertebrates and fish, including their larvae and juveniles. During low tide in the rocky intertidal environment, macroalgal canopies can create moist shelter for sessile and mobile benthic invertebrates (Mathieson *et al.* 1976, Menge 1978, Sapper and Murray 2003). Floating clumps of seaweeds act as a stable habitat for animals in the open ocean. Seaweed clumps harboured significantly higher macrofaunal diversities, densities and biomasses, when compared to the surrounding water column (Vandendriseeche *et al.* 2006). The subtidal brown seaweeds have been studied as habitat for epiphytic fauna extensively along the Atlantic and Pacific Oceans (Edgar 1983b, Taylor and Cole 1994, Russo, A.R., 1997, Taylor 1998a, 1998b, Albertoni *et al.*

2001, Lippert *et al.* 2001, Christie *et al.* 2003). In general, amphipods, isopods, copepods, polychaetes, shrimps, crabs, gastropods, bivalves, sea urchins and fish utilize the seaweed beds, with the gammaridean amphipods, isopods and gastropods representing the most abundant taxa. Marine mammals such as sea otters and sea lions also forage and gain protection from the kelp forests.

Comparatively few investigations on the zooplankton assemblage structure inhabiting seaweeds and seaweed bed have been carried out. In some of these studies, the density and diversity of demersal zooplankton were found to be higher over substrata with macroalgae than in those without, e.g. rock and sand (Alldredge and King 1977, Pakhomov *et al.* 2002, Jara 2005). The settlement and recruitment of invertebrate and fish larvae in seaweed bed have been relatively well studied. The crustose coralline algae in the coral reefs can provide suitable surfaces for the settlement of invertebrate larvae (Adey 1998). These include the economically important sea urchin *Evechinus chloroticu* (Lamare and Barker 2001), blue crab *Callinectes sapidus* (Epifanio *et al.* 2003), Caribbean spiny lobster *Panulirus argus* (Marx and Herrnkind 1985), green-shell mussel *Perna canaliculus* (Paine 1971), and many juvenile fish (Jones 1984, Choat and Ayling 1987, Kingsford 1992). These studies showed that the seaweed beds potentially act as a repository for larval stages and nursery ground of

fishery resources.

1.2.2. Characteristics of Seagrass Habitat and its Associated Faunal Communities

Seagrasses are flowering plants with vascular systems, having true leaves, stems and roots; while seaweeds are collectively referred as macroalgae without vascular systems, true leaves, stems as well as roots. Seagrass beds mostly occur in shallow and sheltered coastal waters anchored in soft substratum, such as sand or mud; whereas most seaweed beds are associated with hard substratum along the coastal waters. Therefore, seagrass and seaweed beds share to a certain extent similarities in structures and the residing environment. Seagrass bed is a desirable habitat for a variety of organisms. The seagrasses and their epiphytic plants serve as a stable source of food (Peterson *et al.* 1984, Lee *et al.* 2001) and provide refuge from predation for many organisms (Heck and Thoman 1981, Heck and Wilson 1987, Summerson and Peterson 1984) by their complex microhabitats (Leber 1985, Gotceitas and Colgan 1989, Jenkins and Sutherland 1997, Boström and Bonsdorff 2000, Hovel and Lipcius 2001). The seagrass bed, especially its canopy, is able to dampen the hydrodynamic action and thus, enhance sediment deposition (Orth 1977, Jackson 1985, Eckman *et al.* 1989, Johnson and Koehl 1994, Pakhomov *et al.* 2002)

and encourage larval recruitment and settlement within the bed (Ekman 1983, 1987, Eckman and Duggins 1991, Irlandi and Peterson 1991, Jenkins and Sutherland 1997, Rooker and Holt 1997, Boström and Bonsdorff 2000). Macroalgae share many similar characteristics with seagrasses as habitats, but their roles have been relatively less well studied. Nonetheless, a number of studies have shown the close relationship between the characteristics of the macroalgal bed and the community structure of its associated fauna. Results of some of these studies are detailed below.

1.2.3. Characteristics of Seaweed Habitat and its Associated Faunal Communities

1.2.3.1. Seasonality

Faunal community structure was found to vary temporally with the phenology, primary production and nutritional value of the seaweeds (Himmelman and Carefoot 1975, Norton and Benson 1983, Buschmann and Santelices 1987, Tugwell and Branch 1989, Edgar 1991a, Steele and Whittick 1991, Edgar 1993, Taylor 1998a, Chavanich and Harris 2002, Danovaro and Fraschetti 2002, Christie *et al.* 2003). Himmelman and Carefoot (1975) revealed that the faunal abundance increased with the host alga biomass, which in turn varied with the algal phenology.

1.2.3.2. Structural complexity

Apart from seasonality, the macroalgal structural complexity has been one of the factors that determine the associated faunal assemblage structure. The composition and size of mobile epifauna are influenced by the algal morphology and growth forms (Taylor and Cole 1994, Lippert *et al.* 2001, Danovaro and Fraschetti 2002, Hauser *et al.* 2006). Seaweed density may also influence the dispersal of epifauna (Taylor 1998b). Biomass of the macroalgae has a positive influence on the density and species richness of the associated macrofauna (Ingólfsson 1995, Albertoni *et al.* 2001, Danovaro and Fraschetti 2002). Moreover, each part of the seaweeds has different habitat properties and so a variety of microhabitats is created by the different plant parts. This provision of heterogeneous habitats has been found to affect the species composition and distribution of the associated macrofauna vertically along the plant (Harkin 1981, Whittick 1983, Christie *et al.* 2003). Therefore, there exists a potentiality of zonation of the faunal assemblage within a single plant.

1.2.3.3. Canopy effect on biota

The existence of seaweed canopies affects the epiphytic faunal assemblages by

altering the density or foraging efficiency of the predators (Menge 1978, Eckman and Duggins 1991, Gagnon *et al.* 2003). The canopy-forming algae also dampen waves and influence water flow (Duggins *et al.* 1990, Ackerman and Okubo 1993) and the associated processes of sedimentation (Eckman *et al.* 1989). Changes in hydrodynamic regimes under macroalgal canopies affect the retention of larvae, recruitment of benthic invertebrates and benthic productivity (Velimirov and Griffiths 1979, Kennelly 1989, Duggins *et al.* 1990, Rodriguez *et al.* 1993, Pakhomov *et al.* 2002). The effects of canopy removal on the macrofaunal abundance and diversity were shown to be considerably significant, with fewer number and species found in the canopy-removed habitat (Bertness *et al.* 1999, Schmidt and Scheibling 2007, Vanella *et al.* 2007).

1.3 Marine Environment and *Sargassum* Communities in Hong Kong

Hong Kong is located in the Indo-West Pacific subtropical region at the northern coast of the South China Sea that covers an area of about 3,500,000 km^2. Its marine environment is affected by monsoons, oceanic currents, and freshwater discharge from the Pearl River. It is heavily influenced by the typical monsoonal climate of the South China Sea. Prevailing in dry season from October to March is the northeast

monsoon, when evaporation losses exceed rainfalls. On the other hand, southwest monsoon can bring in substantial amount of rainfall from April to September, ranging from 188.5mm to 444.6mm on average between 1971-2000 (Hong Kong Observatory 2009). The Taiwan Current from the northeast and the Zhejiang-Fujian Coastal Current bring in cold water to Hong Kong during winter. The Kuroshio Current from the east, together with the Hainan current from the southwest, bring in warm water during summer (Chen 1992, He *et al.* 1994, Chan 1995, Lee and Chen 2003). Therefore, the waters of Hong Kong are kept relatively cold during winter with seawater temperature ranging from 12 to 14°C. However, the maximum temperature in summer could be around 30°C. These resulted in the strong seasonality in Hong Kong seaweed abundance, which reaches its peak in winter and early spring and with most species disappearing in the hot summer (Hodgkiss and Lee 1983, Hodgkiss 1984). Largely due to the influence of the freshwater discharge from the Pearl River in the west, there is a gradient in salinity and turbidity from the west to the east. The western waters of Hong Kong are more estuarine and turbid, and the west coast is more protected from the oceanic currents and monsoons. The western shore is therefore mainly characterized by soft mud flats and mangrove forests with relatively low seaweed diversity. In contrast, the eastern waters are more oceanic and clear. The eastern coastline is subjected to relatively greater wave exposures from currents and

monsoons and hence has more rocky shores with large boulders (Morton and Morton 1983). The presence of stable hard substrata supported more extensive distribution of seaweeds (Hodgkiss and Lee 1983) which included both the temperate and tropical species (Ang 2005).

Approximately 300 species in 122 genera of algae have been reported from Hong Kong (Ang 2005). Among these seaweeds, species of *Sargassum* are the largest brown macroalgae known. There are more than 400 species of *Sargassum* in the world (Yoshida 1983). They are widely distributed in both intertidal and shallow subtidal rocky areas in both tropical and temperate waters.

The thallus of *Sargassum* consists of a root-like holdfast for anchorage on hard substratum and a short primary axis with several long slender laterals that extends vertically from the holdfast. Leaf-like fronds arising from the laterals are the major sites of gaseous exchange, nutrient diffusion and photosynthetic activity. Vesicles located along the laterals at the base of the fronds help the plant maintain a roughly vertical posture to obtain maximum illumination. The strong perennial holdfast facilitates the anchorage of *Sargassum* on exposed intertidal and subtidal zones. The rapid growth of the annual fronds forms dense canopy that creates a large and stable

Sargassum bed as habitats for various marine organisms. However, the ecological value of *Sargassum* spp. as a habitat in the marine ecosystem is not well documented.

In Hong Kong, although information on the phenology, physico-chemical properties, genetic composition and nutrient content of some *Sargassum* spp. are available (Wong 2000, Wong and Cheung 2001a, 2001b, Chan 2002, Cheang 2003, Ang 2006), ecological studies on this genus are still very limited especially for subtidal species like *Sargassum siliquastrum*. There was only one single study on the mobile epiphytic faunal community in *Sargassum henslowianum*, an intertidal species in Hong Kong (Lee 2000).

1.4 Study Organism: the *Sargassum siliquastrum*

Among the 28 species of *Sargassum* identified in Hong Kong (Tseng 1998), *Sargassum siliquastrum* is one of the most abundant (Fig. 1.1). This species is characterized by its strong retroflex basal, lower leaves and secondary branches. The basal part of the main axis thus displays a very peculiar zig-zag appearance. The basal leaves are long and board with entire margins while the middle leaves are more serrated or toothed at the margins. Upper leaves are usually very narrow, with curved

teeth sometimes extended to the midrib. The receptacles are located on the axil of subtending leaves. Male receptacles of this species are elongated and more cylindrical while female receptacles are shorter, flattened and rounded at the apex (Lu and Tseng 1984, Tseng 1998). This species is also widely distributed in Japan, Korea and mainland China. The vertical distribution of this species in Hong Kong ranges from shallow subtidal area of around 3 m below Chart Datum (CD) to deeper subtidal area of -10 m CD. This species is the dominant *Sargassum* species found in the deeper waters in Hong Kong.

The major environment factors affecting benthic macroalgae are light, temperature, salinity, water motion, and nutrient availability. Competition, predator-prey and basiphyte-epiphyte relationships are amongst the most important biological interactions. Individual patterns of growth, morphology, and reproduction are results of overall effects of the combined abiotic and biotic factors (Lobban and Harrison 1994). *Sargassum* populations typically exhibit a seasonal cycle of growth, reproduction, senescence and die-back (De Wreede 1976, Ang 1985, 2006). The phenology and seasonality of *Sargassum siliquastrum* have been illustrated by Chan (2002), Ang (2006) and Yeung (2009). A seasonal cycle of slow growth started from March to August, with rapid growth from September to November, and the plants

attain the reproductive stage from December to January and die-back stage from January to February.

1.5 Study Significance and Objectives

Due to their high economic values, seaweeds have been extensively cultivated or harvested from the wild. In California, the kelp canopies are mechanically harvested in large quantity for their valuable alginates (Steneck et al. 2002). The impact of seaweed harvesting is similar to that produced by physical or biological disturbances. These disturbances remove, totally or partially, the dominant population and modify the distribution and abundance of associated faunal species (Vásquez and Santelices 1984, Vásquez 1995), resulting in highly unstable faunal community (Foster and Barilotti 1990). Harvesting of seaweeds may result in little regeneration of plant tissue (Vásquez and Santelices 1990), reduction in seaweed reproductive output (Sharp and Pringle 1990) and even deforestation that shifts the community from macroalgae-dominated to barren grounds dominated by crustose algae and grazers. This would ultimately lead to collapse of the associated food web (Mann, 1982, Steneck et al. 2002). As the impact of seaweed harvesting can be destructive to the macroalgal communities and their associated faunal assemblages, it is essential to

arouse public awareness on the importance of seaweed ecosystem, which is often overlooked when compared with the other marine ecosystems, e.g. coral reef, worldwide. Therefore, it is crucial to generate information on the ecological role of seaweed bed to contribute to the design of strategy in developing a sustainable practice of seaweed harvesting globally, such as in China and other Southeast Asian countries.

In addition, seaweed bed is believed to act as a sanctuary for economically important marine resources. However, in Hong Kong, only one published study on the faunal community structure in intertidal seaweed community by Lee (2000) but no studies in subtidal seaweed beds have been performed. Hence, it is essential to fill in the knowledge gap on the role of seaweed bed as a habitat, especially for the economically important fishery species, in order to contribute to the general understanding of the dynamics of Hong Kong marine environment and its associated faunal communities. Only by collecting the baseline information of seaweed community and its ecological value as animal shelter can one devise a strategy in assessing environmental impacts caused by coastal developments, which are the major threats to the coastal macroalgal communities especially in Hong Kong.

Therefore, the general objectives of this study are as follows:

(1). to identify the faunal assemblage, including zooplankton and epiphytic fauna, in the seaweed bed of *Sargassum siliquastrum* and its temporal variation;

(2). to study the relationship between the faunal structure and the seaweed structural complexity as well as biomass.

The research study is divided into three parts:

Part I: Temporal fluctuation of faunal (zooplankton + epiphytic fauna) abundance in seaweed bed;

Part II: Effects of seaweed canopy on faunal composition and community structure;

Part III: Relationship of faunal diversity and abundance with the structural complexity, in terms of branch number, length, surface area, and biomass of seaweeds.

1.6 Study Sites

The research studies were performed in Lung Lok Shui (LLS) in Tung Ping Chau Marine Park (TPCMP), with Lung Lun Tsui (LLT) (also in TPCMP) and Lo Fu Ngam (LFN) in Sai Kung serving as the replicate sites.

Tung Ping Chau is a bean-shaped island within the TPCMP that covers a sea area of 270 hectares. It is located in the northeastern most part of New Territories in Hong Kong Special Administrative Region (HKSAR) (Fig. 1.2). Because of its distant location from the rest of Hong Kong, human disturbance is less severe compared with other places in HKSAR. The island is made up of layers of sedimentary rocks, providing hard and stable substrata for both corals and seaweeds. Therefore, more than 65 species of algae (Ang *et al.* 2000) and around 65 species of hard coral (Ang *et al.* 2003) have been recorded around this island. For better protection of the rich communities of coral, algae, fishes and marine invertebrates found around this island, it was designated as the fourth marine park in Hong Kong on the 16th of November in 2001. Two core areas were defined where fishing and other destructive activities are strictly prohibited. Limited fishing activities inside the marine park are allowed only for permit holders. Hook-and-line fishing is allowed only within the confine of the recreational fishing areas (Fig. 1.2)

The difference in physical environment between the two sides of the island resulted in the presence of different marine communities. The northwestern side of the island is more sheltered, where two main patches of coral communities can be found in the two core areas of A Ye Wan and A Ma Wan. On the southwestern side of the island, a

rocky shore called Lung Lok Shui can be found. Due to its high exposure to waves, only isolated coral heads can be found in this site and the area is mainly dominated by marine brown algae like *Sargassum* (Ang *et al.* 2000).

At least 65 species of algae were recorded in Tung Ping Chau Marine Park. Among these seaweeds, about 13 species are green algae, 26 are brown algae and 26 are red algae. They are distributed from the intertidal to the shallow subtidal areas along the coast at A Ma Wan, A Ye Wan and Chau Mei Kok during the period from fall to spring. The strong wave action at Lung Lok Shui and Lung Lun Tsui brings adequate nutrients to nourish a higher diversity of algae which may extend to the depth of 10m (AFCD 2006).

Lung Lok Shui (LLS) (114°26'E and 22°33'N) (Fig. 1.2), on the southwestern side of the Tung Ping Chau Island, is characterized with a bed of dolomitic cherty siltstone extending southeast down into the sea for about 100m to a depth of -10m C.D, forming a suitable substratum for the growth of intertidal as well as subtidal seaweeds. The rest of the substratum is mainly composed of layers of sedimentary rocks, boulders and a large sandy area which harbours populations of *Sargassum siliquastrum*. It is exposed to strong waves and currents, especially during the

southeast monsoon in summer. Extensive bed of *Sargassum siliquastrum* can be found that extends to the depth of 10 m.

Lung Lun Tsui (LLT) (114°26'E and 22°32'N) is just adjacent to LLS and is about 300 m away. It thus shares similar environmental conditions with LLS. The substratum is also composed of layers of sedimentary rocks and boulders. An extensive bed of *S. siliquastrum* is found to extend from north to south for 200 meters parallel to the coast in the water regions at -3 to -6 m C.D.

Lo Fu Ngam (LFN) (114°17'E and 22°22' N) (Fig. 1.2) is a small rocky bay opposite to the Port Shelter Island in the Sai Kung area in the eastern Hong Kong waters. The substratum is composed of large rock and boulders, creating space for the attachment of *S. siliquastrum*. Extensive bed of *S. siliquastrum* can be located at the depth of -3 to -6 m C.D.

1.7 Thesis Organization

This thesis is organized into six chapters and the content of each chapter is briefly summarized as follows:

Chapter 1 - General Introduction

This chapter reviews the information on the economical benefits of seaweeds to human societies. Moreover, the ecological role of seaweed beds as habitats for a variety of fauna is briefly discussed. The local seaweed communities in Hong Kong, the study organism and the study sites are briefly described. The rationale as well as the general objectives of this study are also enumerated.

Chapter 2 – Zooplankton Assemblage in Seaweed Bed of *Sargassum siliquastrum* and Its Temporal Variation

This chapter illustrates the community structure of the zooplankton assemblage found in the seaweed bed of *Sargassum siliquastrum* and how it changed with seasons. The temporal association between zooplankton assemblage and seaweed phenology was displayed. Moreover, the role of *Sargassum siliquastrum* bed as nursery and nesting ground of economically as well as ecologically vital zooplankton species was highlighted.

Chapter 3 – Effects of Seaweed Canopy on the Structure of Zooplankton Assemblage in the *Sargassum siliquastrum* Bed

This chapter describes the effects of canopy removal on the abundance and species diversity of zooplankton assemblage by comparing the zooplankton community structure in treatment (i.e. canopy elimination), control (i.e. canopy intact) and unvegetated environment.

Chapter 4 – Epiphytic Faunal Assemblage in Seaweed Bed of *Sargassum siliquastrum* and Its Temporal Variation

This chapter presents changes in the community composition of the epiphytic faunal assemblage associated with the seaweed bed of *Sargassum siliquastrum* over time. The impacts of environmental factors on faunal assemblage were assessed. Furthermore, the function of *Sargassum siliquastrum* bed in larval settlement, and as nursery and nesting ground of fishery resources was stressed in all seaweed growth stages.

Chapter 5 – Relationship of Epiphytic Faunal Assemblages with the Structural Complexity of the Seaweed *Sargassum siliquastrum*

This chapter reveals the connection between epiphytic faunal assemblage structure with physical properties, such as length, branch number and biomass, of *Sargassum siliquastrum*. The within-plant faunal zonation in *Sargassum siliquastrum* was also exhibited.

Chapter 6 – Summary and Conclusion

This chapter summarizes the findings of the present study to identify the faunal assemblage in the seaweed bed of *Sargassum siliquastrum,* and the relationship between faunal and seaweed structures. The ecological importance of seaweed beds as a habitat is emphasized with a call for their greater appreciation and protection.

Fig. 1.1 Habit of *Sargassum siliquastrum* (Turn.) Ag. (Adopted from Chan 2002)

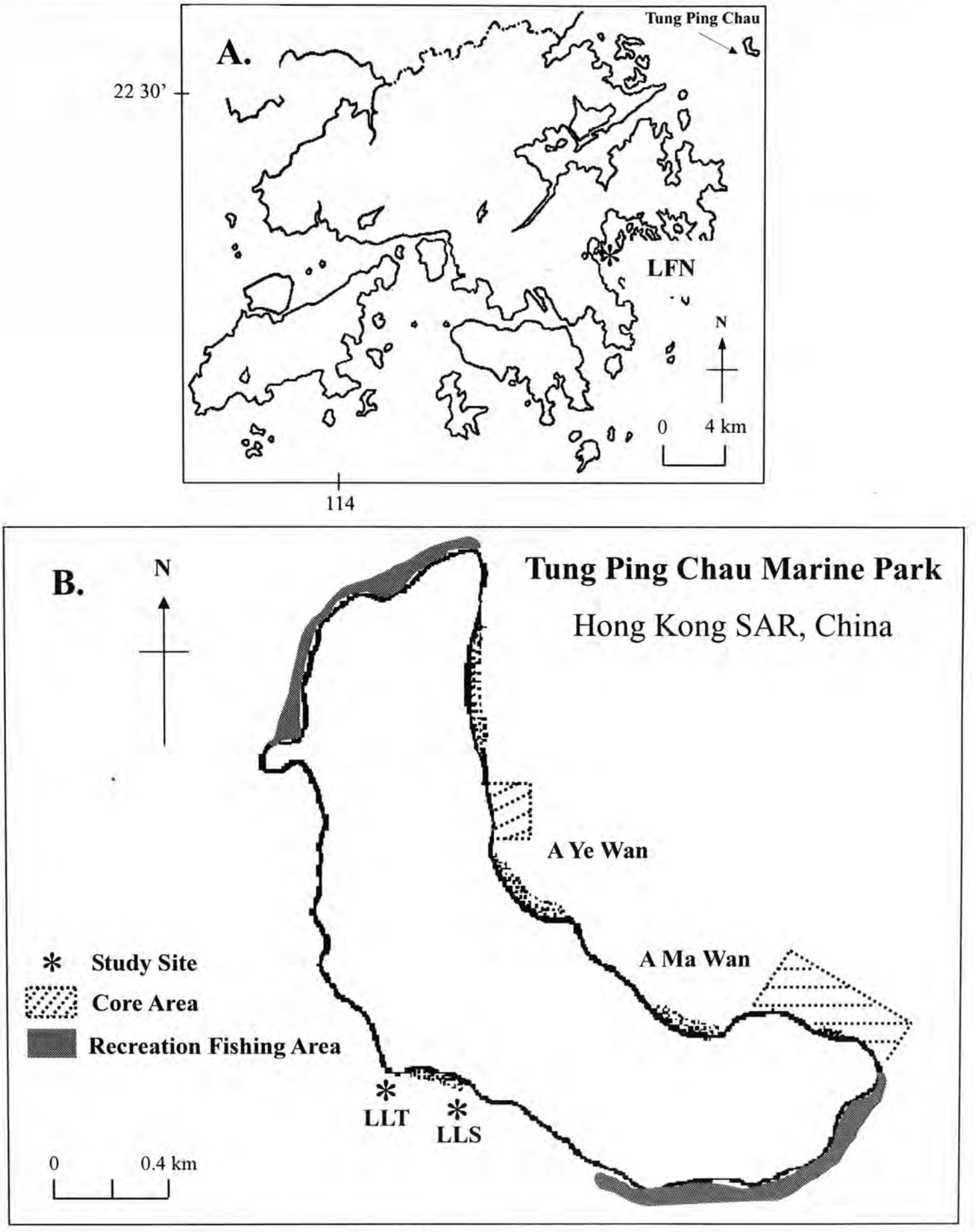


Fig. 1.2 Map of **A.** Hong Kong and **B.** Tung Ping Chau Marine Park showing the locations of the three study sites – Lung Lok Shui (LLS) and Lung Lun Tsui (LLT) in Tung Ping Chau Marine Park as well as Lo Fu Ngam (LFN) in Sai Kung (Modified from Ang *et al.* 2005).

Chapter 2

Zooplankton Assemblage in Seaweed Bed of *Sargassum siliquastrum* and Its Temporal Variation

2.1 Introduction

Hong Kong is located in the northern South China Sea, within the Indo-West Pacific subtropical region. Variation in zooplankton abundance and species composition with seasons as well as space in Hong Kong waters is mainly brought about by the prevailing monsoons, the subsequent water mass movement and discharge from the Pearl River. The South China Sea is in a typical monsoonal climatic zone. The climate of Hong Kong is thus quite significantly affected by it. Prevailing in dry season from October to March is northeast monsoon, while in wet season from April to September is southwest monsoon. Under the action of seasonal monsoons, the water mass movement is carried along the Guangdong coast. In winter, the coastal waters of Hong Kong are subjected largely to the influence of the Zhejiang-Fujian Coastal Current, and to a lesser extent, the Kuroshio Current (Lee and Chen 2003). The water mass is then expanded along the coasts from northeast to southwest under the influence of the

northeast monsoon, carrying along with it such species as *Calanus sinicus*, *Pseudeuphausia sinica*, *Sagitta crassa* into the northern South China Sea. These species, being distributed along the coasts of South China, including Hong Kong, only occur in winter and spring. *Calanus sinicus* has been known to be a common temperate copepod (Chen *et al.* 1985, Zheng and Li 1988, Huang *et al.* 1992) and is widely regarded as indicator species of the Zhejiang-Fujian Coastal Current (Huang *et al.* 1992, Hwang and Wong 2005). In addition, some warm-temperate species, e.g. *Sagitta crassa*, *Centropages tenuiremis* (Huang *et al.* 1997), also enter these coastal waters carried by the Zhejiang-Fujian longshore current. Their abundance varies seasonally with the alternation of monsoons. In summer, the coastal water mass along the Guàngdong shore receives a great amount of freshwater from the Pearl River on one hand, and is also pressed and permeated by open sea water masses at the outer boundary on the other. Therefore, the composition of zooplankton populations in the Hong Kong coastal community is relatively more complex during summer times. In the waters along the coast of Hong Kong, salinity decreases significantly to a level lower than 30.0 ppt. At the same time, water temperature rises. The coastal water abounds with nutrition (Chau and Wong 1960, Chau 1962, Watts 1973, Chiu *et al.* 1985), favouring the development of plankton (Nixon 1988, Ware and Thomson 2005, Frank *et al.* 2006). In this period, no Zhejiang-Fujian coastal warm-temperate typical

species can be seen in the populations of the coastal water mass. Those that occupy the water mass are mostly tropical low-haline species that can adapt to low salinity, such as *Acartia erythrae*, *Calanopia thompsoni*, *Tortanus dextrilobatus*, *Pseudodiaptomus poplesia*, *Lucifer hanseni* and *Labidocera euchaeta*. Medium-haline offshore populations occurring in the mixing zone where the offshore water invades the coastal water can also be found, such as *Sagitta nagae* and *Temora turbinata*; as well as high-haline species, e.g. *Subeucalanus subcrassus*, *Euchaeta concinna*, *Undinula vulgaris*, *Lucifer typus*, and *Sagitta enflata* (Chen 1992, He *et al.* 1994, Chan 1995, Lee and Chen 2003). Due to the runoff of the Pearl River, the eastern and southern coasts of Hong Kong showed a great diversity of zooplankton while a lower diversity of species was found nearby the mouth of the Pearl River (Chen 1980, 1992).

Investigations on the substratum preference of zooplankton showed that emergence of zooplankton associated with the substratum occurs in many types of near shore habitats, including sandy bottoms (Takahashi and Kawaguchi 1997, Thistle 2003), subtidal seagrass beds (Youngbluth 1982, Bell *et al.* 1988, Jacoby and Greenwood 1989, Walters 1991 Walters and Bell 1994), coral reefs (Alldredge and King 1977, Porter *et al.* 1977, Jacoby and Greenwood 1988, 1989, Grutter *et al.* 2000), algae and

stones (Oishi and Saigusa 1999), and kelp beds (Manner 1981). Enhanced densities of the demersal and pelagic zooplankton were correlated with structurally complex subtrata (e.g. coral reefs, seagrass beds) (Alldredge and King 1977, Porter *et al.* 1977, Jacoby and Greenwood 1988, Boström and Bonsdorff 2000). Aquatic vegetation could facilitate the retention of invertebrate and fish larvae, thus their recruitment and settlement within the bed (Ekman 1983, 1987, Eckman and Duggins 1991, Irlandi and Peterson 1991, Ray and Stoner 1995, Jenkins and Sutherland 1997, Rooker and Holt 1997, Bologna and Heck 1999, Boström and Bonsdorff 2000, Lamare and Barker 2001, Pakhomov *et al.* 2002, Epifanio *et al.* 2003, Gamfeldt *et al.* 2005, Pershing *et al.* 2005, King and Sheridan 2006, Vanella *et al.* 2007). Therefore, it is inferred that the more structurally complex substratum, e.g. macroalgal bed, can potentially act as a suitable repository for fishery resources.

Assemblages of zooplankton are valuable resources in marine ecosystem and in human economies. Amphipods, copepods, mysis and arrow worms, for examples, are important natural food sources to invertebrates and fishes (Emery 1968, Alldredge and King 1977, Chen 1980, 1992, Alheit 1981, Fancett and Kimmerer 1985, Talbolt and Baird 1985, Leber 1985, Nagasawa 1991, Bullard and Hay 2002, Freseriksen *et al.* 2006) and are extensively used as feeds in aquaculture of seahorse and fish (Chen

1992, Chen and Shi 2002, Drillet *et al.* 2006, Ren 2006). They are also used as poultry feed accessory (Chen 1992). Moreover, zooplankton can be directly consumed by human due to their high protein, lipid and trace element contents. Chen (1992) stated the annual fishery production of copepods to be of several thousand tonnes in the Guangdong Pearl River drainage system. There is also a maximum production of up to 100,000 tonnes per year of the sergestid *Acetes* fishery in Bohai, China. Mysids and copepods are used in the manufacture of traditional preserved shrimp paste and oil in China. On top of these, zooplankton are key water mass indicators in hydrological, oceanographic and fisheries studies (Chen 1980; Bullard and Hay 2002; Gislason and Astthorsson 2004; Xiao 2004; Frederiksen et al. 2006). Chen and Shi (2002) reported that schooling of fish was found to be correlated with the presence of hyperiidean. Zooplankton can also be used in biological control. For example, the cyclopoid copepods were effectively used in mosquito control in the marsh fields (Marten et al. 1994).

Despite the potential of seaweed beds as nursery grounds of economically important fisheries, only a small number of dedicated research studies on zooplankton assemblage have been carried out in kelp beds in temperate region (e.g. Hammer 1981; Gaines and Roughgarden 1987; Pakhomov et al. 2002) or in seagrass beds in more

tropical seas (Boström and Bonsdorff 2000; Lamare and Barker 2001; Gamfeldt et al. 2005; Pershing et al. 2005), but not in beds of other macroalgal groups such as the brown seaweed *Sargassum* spp. in more subtropical regions worldwide. The importance of subtropical areas as a refuge for tropical species is becoming more apparent given the imminence of global warming and climate change. This will likely be true for zooplankton assemblages, especially those made up of tropical species. Not much, however, is known about the subtropical plankton assemblages and their association with the substrata, e.g. the seaweed (macroalgae) beds. Very few published investigations on zooplankton community structure and abundance have been reported from Hong Kong (e.g. Chen 1980, Wong et al. 1993, Lee and Chen 2003). İn 1980, a preliminary survey of the zooplankton fauna yielded 120 species in the coastal waters south and west of Hong Kong. The coastal zooplankton consisted mainly of estuarine and neritic species, in which members of Copepoda were most abundant in terms of numbers and species whereas members of Chaetognatha ranked second in abundance (Chen 1980). No clear seasonal patterns of Calanoida and Cyclopoida were detected in the study of planktonic copepods of Tolo Harbour, in the northeastern part of Hong Kong (Wong *et al.* 1993). In the 2000s, 151 marine planktonic species, distributed among 31 families, were recorded from studies in Hong Kong waters (Lee and Chen 2003). The association of zooplankton assemblages

with the seaweed community has never been investigated in Hong Kong nor in other subtropical areas in the Indo-West Pacific as a whole.

In terms of community structure, factors influencing the dynamics of the zooplankton assemblages are complex. These factors include variations in food sources (Huang *et al.* 1989, 1997, 2004, Wong *et al.* 1990, Fu *et al.* 1995, Yin *et al.* 1995, Gasol *et al.* 1997, Martinez- Corfova *et al.* 1998, Calbet 2001, Danovaro and Fraschetti 2002, Coman *et al.* 2003, Ware and Thomson 2005, Martin *et al.* 2006), trophic links like predation (Newsbury 1972, Omori and Hamner 1982, Thistle *et al.* 1984, Leber 1985, Owen 1989, Ashjian and Wishner 1993, Bullard and Hay 2002, Gislason and Astthorsson 2004), physical and chemical water quality parameters (Godoy and Coutinho 2002) and kelp bed seasonality and its phenology (Godoy and Coutinho 2002, King and Sheridan 2006). No general patterns can thus far be established indicating the controlling factors underlying the zooplankton assemblage structure. The relationship between environmental parameters and the zooplankton assemblage structure may be site-specific.

Many coastal areas in the subtropical Indo-West Pacific region are dominated by seaweed beds made up primarily of the brown algae *Sargassum* spp. To fill in the

knowledge gap of the role of macroalgal bed as feeding and nursery grounds for zooplankton, which is considered potentially as desirable habitat for zooplankton due to its highly complex structure, extensive bed of *Sargassum siliquastrum* was chosen as a subject of this current study to determine, both qualitatively and quantitatively, its function as zooplankton habitat. The relationship between environmental parameters as well as seaweed phenology and the zooplankton assemblage structure was investigated. This study is the first to provide evidences on the potential of subtropical beds of *Sargassum siliquastrum* as a nursery and nesting ground for zooplankton assemblages.

2.2 Materials and Methods

2.2.1 Sample collection

Zooplankton samples were collected from two sites: Lung Lun Tsui (LLT) and Lo Fu Ngam (LFN), from November 2006 to January 2008. Sample collection was done once every two months from September to February during the rapid growth, reproductive and dieback stages of *Sargassum siliquastrum* and once every three months from March to August during its slow growth stage (Chan 2002, Ang 2006,

Yeung 2007). Each sampling was carried out around the full moon of the sampling month to ensure that the zooplankton samples were subject to the influence of similar tidal and lunar cycles (Alldredge and King 1980, Bell *et al.* 1988, Jacoby and Greenwood 1988, Walters 1988, Oishi and Saigusa 1999, Saigusa and Oishi 2000, Jara 2005).

During each sampling, a reference transect of 30 m in length was first laid in the *Sargassum* bed. A zooplankton net (mesh size 335μm, 15cm ring radius) was then hauled close to the substratum for a distance of 20 m 5 min after the reference transect was laid. Hand-net tow was chosen as it was shown to yield consistently more zooplankters m^{-2} in terms of abundance and species diversity with minimal bottom disturbance than other sampling methods, such as net tows, sled-net and emergence trap (Jara 2005). During each sampling, hand-net towing was conducted three times each over vegetated (i.e. bed of *Sargassum siliquastrum*) and unvegetated area (i.e. barren ground made up of boulders close to the seaweed bed) in each site. However, persistent low underwater visibility prevented effective sampling in January 2007 at LLT, so that only two samples over vegetated area were collected. After each haul, the net was emptied, rinsed with minimal amount of filtered seawater and its contents placed in white sampling bottles and preserved with a few drops of 35% formalin

solution.

During the sampling period, density of *Sargassum siliquastrum* was measured. This was done by placing eight 0.5m x 0.5m quadrats haphazardly over the seaweed bed and counting all individuals found within each quadrat. Moreover, the sea surface temperature, salinity and dissolved oxygen levels were recorded using a portable multi-meter (Model 85, YSI Inc., USA).

2.2.2 Data acquisition

All preserved zooplankton were identified to the possible lowest taxon level and their density counted using a dissecting microscope. Effort was concentrated on dominant groups of zooplankton. For certain taxa, further classification was made based on their life history stages, such as larvae, nauplii and adult.

Zooplankton density was standardized and expressed as number of individuals per m^3 seawater filtered to allow comparisons between samples collected over vegetated and unvegetated substrata. Diversity was calculated and expressed as species richness, i.e. number of species and zooplankton taxa recorded in each tow, Shannon Diversity

Index H' (Margalef 1958, Pielou 1966, 1975, Hurlbert 1971) or Evenness Index J (Margalef 1958, Pielou 1966, Hurlbert 1971). Mean density, species richness, Shannon Diversity Index H' and Evenness Index J were reported with standard deviation. The proportional abundance (%) of the most common zooplankton groups collected from vegetated and unvegetated habitats was compared by calculating the number of individuals belonging to the same taxonomic group over the total number of individuals counted. Association degree of the common groups was obtained by calculating the mean percentage of number of individuals in vegetated or unvegetated habitat in proportion to the total abundance of that group in both vegetated and unvegetated habitats, i.e. in equation form:

$$\text{Association degree of taxon N in vegetated or unvegetated habitat (\%)} = \left(\frac{\#\text{ N (in vegetated or unvegetated habitat)}}{\text{Total \# of N in both habitats}}\right)(100)$$

2.2.3 Data analysis

From November 2006 to January 2008, a total of 20 and 21 zooplankton samples were obtained from vegetated and unvegetated habitats respectively for data analyses. All statistical analyses were performed using SPSS 13.0 for Windows (SPSS Inc., USA). All data were tested for normality by Kolmogorov-Smirnov test and for

homogeneity of variance by Levene Median test. Transformation of the data was carried out if the parametric assumptions were not met. Non-parametric analyses were used instead if transformations of data still failed to satisfy the assumptions of parametric statistics. The significance level (p value) of all statistical analyses was set at 0.05.

One-way ANOVA or Kruskal-Wallis test was carried out to compare the temporal changes in mean zooplankton density, species richness, Shannon Diversity Index H' and Evenness Index J, while Two-way ANOVA or Friedman test was employed to evaluate the among-site difference in seaweed density and length. In addition, either parametric t-test or non-parametric Mann-Whiney U test was used to evaluate the effects of between-habitat (i.e. vegetated against unvegetated) difference on zooplankton abundance, species richness, Shannon diversity Index H' and Evenness Index J in each sampling month. Relationships between zooplankton assemblage and environmental parameters as well as seaweed phenology were assessed by regression analyses.

The zooplankton community structure in terms of species abundance and composition of each monthly tow over the vegetated and unvegetated beds in each site were

expressed in non-metric multidimensional scaling (MDS) ordination. The similarity among tows was evaluated using cluster analysis based on Bray-Curtis similarity measure with 1000 times of permutation by SIMPROF. Two-dimensional MDS plots were displayed to show the structure of the zooplankton assemblages. In cases where the stress value of the 2-dimensional plots was larger than 0.20, a 3-dimensional MDS plot was shown instead. ANalysis Of SIMilarities (ANOSIM) was used to test for significant differences ($p<0.05$) between groups and SIMilarity of PERcentages (SIMPER) procedure was used to identify the discriminating taxa between them. The abundance data were standardized and fourth-root transformed prior to the analyses to minimize the effect of the exceptional abundant groups (e.g. calanoid copepods, gammaridean juveniles). All analyses on the zooplankton community assemblages were conducted using PRIMER v. 6 (Clarke and Warwick 2006).

2.3 Results

2.3.1 Temporal Change in Zooplankton Assemblage Composition

Throughout the sampling period, a total of 72 species and/or taxonomic groups of zooplankton were recorded in both sites, with 57 identified in LFN (Table 2.1) and 63

in LLT (Table 2.2). Anomuran larvae, the calanoids *Pseudodiaptomus* spp. and *Paracalanus* spp., the cyclopoid *Oithona rigida*, fish larvae of family Monacanthidae and *Petroscrites breviceps*, mysis unidentified 1 and *Mysidopsis indica* were only encountered in LFN, whereas the sergestid larvae, calanoids *Tortanus gracilis, Calanopida elliptica* and *Centropages orsinii,* cyclopoid *Microsetella norvegica,* poecilostomatoid *Cymbasoma* spp., fish larvae of *Sebastiscus marmoratus,* isopod juvenile, mysid *Anisomysis ijima* and *Iiella ohshimai,* cumacean and ostracods were recorded only in LLT.

As an initial analysis, zooplankton samples from both vegetated and unvegetated habitats from all the sampling months were pooled. This approach resulted in an indistinct grouping of zooplankton assemblage between vegetated and unvegetated habitats in LFN (Figure 2.1) and in LLT (Figure 2.2). Thereafter, a more detailed analysis on the dataset was carried out on samples from vegetated and unvegetated habitats collected over different sampling times.

In LFN, the mean zooplankton assemblages among the sampling months were statistically significantly different in both vegetated (Figure 2.3) and unvegetated (Figure 2.4) habitats. Significantly distinct grouping of zooplankton assemblages

among different sampling months were also observed in the vegetated (Figure 2.5) and unvegetated (Figure 2.6) habitats in LLT. Hence, there existed a significant temporal variation in the zooplankton community structure, with the difference being more pronounced in vegetated habitat. In addition, inter-annual disparity in zooplankton community composition was detected in both vegetated and unvegetated habitats in LFN (Figures 2.7 and 2.8) as well as in LLT (Figures 2.9 and 2.10). The structure of the zooplankton assemblages was different between years, as indicated by its non-cyclical pattern in the MDS ordination plot wherein the zooplankton assemblage structure of the same month between years did not shift back to the same position as that in the previous year. There were distinct discriminating species among different sampling months in both LFN (Table 2.3) and LLT (Table 2.4). In general, in vegetated habitat at both sites, gammarideans of the family Synopiidae, mysid juvenile, the calanoids *Acartia erythrae*, *Temora turbinata*, *Pseudodiaptomus incisus* and *Paracalanus parvus* were the major contributors to differences between sampling months. In the unvegetated habitat, the major differentiating species among sampling months included mysid juvenile, the calanoids *Acartia erythrae*, *Temora turbinata*, *Subeucalanus subcrassus* and *Paracalanus parvus*.

In the vegetated habitat in both sites, the MDS plot (Figure 2.11 A) and ANOSIM

analysis (Table 2.5) indicated that mean zooplankton assemblages between sites were significantly different at most sampling months. The mysid juvenile, the calanoids *Pseudodiaptomus incisus, Paracalanus parvus* and the cirripeds were the major contributors to these differences (Table 2.5). At the level of 40% similarity, the cluster dendrogram (Figure 2.11 B) revealed eight clusters of zooplankton assemblages representing: (1). Jun07 and Sep07 of LFN; (2). Nov06, Mar07, Jun07 and Nov07 of LLT; (3). Nov06 and Nov07 of LFN; (4). Jan07 of LFN and LLT; (5). Jan08 of LFN; (6). Sep07 of LLT; (7). Mar07 of LFN; and (8). Jan08 of LLT. Among these eight clusters, four major statistically significant groupings consisting of (1), (2), (3)-(5) and (6)-(8) were detected. For the unvegetated patch in both sites, significantly distinct grouping of zooplankton assemblages between the two sites at different times could also be detected (Figure 2.12A, Table 2.6). The major differentiating taxa between sites included the mysid juvenile, the calanoids *Acartia erythrae, Temora turbinata* and *Paracalanus parvus* (Table 2.6). The cluster dendrogram (Figure 2.12 B) revealed six clusters at a similarity level of around 40%, representing (1). Jan07 Mar07 of LFN and Jan07 of LLT; (2). Mar07 of LLT; (3). Jan08 of LFN and LLT; (4). Nov06 and Sep07 of LFN; (5). Jun07, Nov07 of LFN and Nov06 of LLT; and (6). Jun07, Sep07 and Nov07 of LLT. However, these cluster groupings were not of statistical significance.

2.3.1.1 Change in Zooplankton Abundance with Time

Throughout the sampling period in LFN, a total of 1503 zooplankters per m^3 were identified in vegetated habitat while 1354 were identified in unvegetated habitat. The mean (± S.D.) zooplankton density in vegetated habitat was 71.58 ± 57.97 ind. m^{-3} while that in unvegetated habitat was 64.47 ± 39.60 ind. m^{-3}. The zooplankton density changed over time (Figure 2.13). In the vegetated patch, the zooplankton density experienced a relatively low level below 40 ind. m^{-3} from Nov06 to Mar07. The density then increased and reached its peak at 242.04 ± 244.83 ind. m^{-3} in Sep07. The peak was followed by a drop to the previous low level at around 40 ind. m^{-3} and the density remained relatively unchanged till the end of the sampling period. For the zooplankton density in unvegetated habitat, the trend was similar to that in vegetated habitat, except that the maximum density reached a level of 162.30 ± 105.45 ind. m^{-3} in Jun07. There was a significant temporal variation in mean zooplankton density in unvegetated habitat (Kruskal-Wallis test, df=6, p=0.012) but not in vegetated habitat (Kruskal-Wallis test, df=6, p=0.161).

In LLT, a total of 3167 zooplankters per m^3 were found in vegetated habitat while 2148 were found in unvegetated habitat. Across the sampling period, the mean (± S.D.)

zooplankton density in vegetated habitat was 150.79 ± 155.40 ind. m^{-3} while 102.28 ± 39.33 ind. m^{-3} was recorded in unvegetated habitat. In the vegetated habitat (Figure 2.14), the zooplankton density remained at a relatively low level below 35 ind. m^{-3} from Nov06 to Jan07. The density then increased and reached its highest peak at 392.55 ± 607.15 ind. m^{-3} in Jun07. This was followed by a drastic decline to an even lower level at about 15 ind. m^{-3} in Sep07. Since then, a dramatic rise to the second highest peak at 310.69 ± 373.94 ind. m^{-3} was observed in Nov07 and the density returned to its previous low level of about 30 ind. m^{-3} in Jan08. For the mean zooplankton density in unvegetated habitat, the trend was also similar to that in vegetated habitat, except that its highest peak at 258.79 ± 23.56 ind. m^{-3} was spotted in Nov07 while its second highest peak at 147.68 ± 22.67 ind. m^{-3} in Jun07. A significant temporal change in zooplankton density was detected in unvegetated habitat (Kruskal-Wallis test, df=6, p=0.039) but not in vegetated habitat (Kruskal-Wallis test: df=6, p=0.058).

2.3.1.2 Temporal Change in Zooplankton Species Composition

For the mean (± S.D.) species richness in vegetated habitat in LFN (Figure 2.15 A), a slight increase from 7.33 ± 4.93 to 11.33 ± 4.93 taxa was observed from Nov06 to

Jan07. A drop to a lower level followed and remained relatively constant at about seven taxa from Mar07 to Jun07. In Sep07, a plunge to the minimum at 4.33 ± 2.52 taxa was spotted while the species richness experienced a rise to the maximum at 15.67 ± 2.08 taxa in Nov07. The level then returned to a lower level at 10.00 ± 1.00 taxa in Jan08. The trend in unvegetated habitat was more or less the same as that in vegetated habitat, except that the lowest point at 5.33 ± 4.51 taxa was recorded in Nov06 and the highest was recorded at 11.00 ± 2.00 taxa in Jan07. A significant difference in mean species richness over time was detected in vegetated habitat (Kruskal-Wallis test: df= 6, $p<0.05$) but not in unvegetated one (ANOVA: df=20, $p>0.05$).

The pattern in mean (± S.D.) Shannon-Weiner diversity index (H') in both habitats (Figure 2.16 A & B) varied similarly as that in species richness. In vegetated habitat, H' reached its maximum at 2.32 ± 0.12 in Nov07 and its second highest at 2.12 ± 0.29 in Jan07. The value of H' ranged from 0.18 ± 0.12 to 2.32 ± 0.12 in vegetated habitat and from 0.26 ± 0.12 to 1.63 ± 0.16 in unvegetated habitat. Significant temporal variation in H' was obtained in both habitats (Kruskal-Wallis test: df=6, $p<0.05$). Mean Species Evenness (J) fluctuated in a similar way as H' in both habitats (Figure 2.16 A & B). The range of mean (± S.D.) J was from 0.18 ± 0.19 to 0.90 ± 0.04 in

vegetated patches and from 0.13 ± 0.06 to 0.78 ± 0.15 in unvegetated patches. Significant temporal variation in J was found in both habitats (Kruskal-Wallis test: df=6, $p<0.05$ for vegetated habitat; ANOVA: df=19, $p<0.05$ for unvegetated habitat).

Figure 2.15 (B) shows the temporal change in mean (± S.D.) species richness in both vegetated and unvegetated patches at LLT. In the vegetated habitat, a drastic rise from the minimum of 8.67 ± 5.51 taxa to the highest peak of 28.00 ± 1.00 taxa was recorded from Nov06 to Mar07. A decrease to a previous low level of 9.00 ± 2.00 taxa followed from Mar07 to Sep07. The species richness then increased to the second highest level at 21.67 ± 0.58 in Nov07, but then returned to a lower level at 12.67 ± 2.52 in Jan08. The species richness in unvegetated habitat fluctuated in a similar fashion as that in vegetated habitat, with the maximum at 17.00 ± 4.58 taxa spotted in Mar07 and the second highest at 14.67 ± 3.51 taxa in Nov07. However, the lowest point at 6.67 ± 4.04 taxa was attained in Jan07. Significant temporal difference in species richness was detected in both vegetated and unvegetated habitats (ANOVA: df=19, $p<0.05$ for vegetated habitat; ANOVA: df=20, $p<0.05$ for unvegetated habitat).

The trend in mean Shannon-Weiner diversity index (H') (Figure 2.16 C & D) in both habitats varied similarly as that in species richness, the exception being that in

vegetated habitat, mean (± S.D.) H' reached its maximum at 2.09 ± 0.25 in Jan07. The values of H' ranged from 0.97 ± 0.60 to 2.09 ± 0.25 in vegetated habitat while from 0.84 ± 0.20 to 1.69 ± 0.44 in unvegetated habitat. Significant temporal variation in H' was only found in unvegetated habitat (ANOVA: df=20, $p<0.05$). Mean evenness index (J) changed analogously with H' in both habitats. The range of mean (± S.D.) J was from 0.45 ± 0.29 to 0.86 ± 0.05 in vegetated habitat while from 0.35 ± 0.09 to 0.81 ± 0.10 in unvegetated habitat. Significant temporal variation in J was only found in unvegetated habitat (ANOVA: df=20, $p<0.05$) (Figure 2.16 C & D).

2.3.2 Effects of Vegetation on Zooplankton Assemblage Structure

2.3.2.1 Comparison between Vegetated and Unvegetated Habitats in terms of Zooplankton Community Structure

Given the significant temporal difference in zooplankton assemblages in both vegetated and unvegetated habitats mentioned in section 2.3.1, further analyses were performed to investigate the effects of vegetation on zooplankton community structure in each sampling month in each site.

The MDS plot (Figure 2.17) generally revealed separate grouping of zooplankton assemblages between vegetated and unvegetated habitats in each sampling month in LFN, though these separations were not statistically significant. The between-habitat differences were more apparent in Jan07, Mar07, Sep07, Nov07 and Jan08, as reflected by their higher global-R values obtained in ANOSIM (Figure 2.17). This pattern was further confirmed by clustering into two separate groups at a level of similarity of around 40%, of samples from the vegetated and unvegetated habitats respectively (Figure 2.18). The gammaridean of family Synopiidae, the gammaridean juvenile, the mysid juvenile, the calanoids *Acartia erythrae, Temora turbinate* and *Pseudodiaptomus incisus* were the major differentiating taxa between vegetated and unvegetated habitats in the respective sampling month in LFN. Figure 2.19 shows the population dynamics of these discriminating taxa. Gammaridean amphipod and the calanoid *Pseudodiaptomus incisus* were more abundant in the vegetated habitat over time, while the calanoids *Acartia erythrae* and *Temora turbinate* and the mysid juvenile were more numerous alternatively in both habitats at certain time period. Significant variation in abundance of these taxa between habitats was detected in specific months, e.g. *Acartia erythrae* in Jan07 and Jan08 (Mann-Whitney test: $p<0.05$), *Pseudodiaptomus incisus* in Nov07 (*t*-test: $p<0.05$) and mysid juvenile in Jan08 (Mann-Whitney test: $p<0.05$). Large local aggregation of individuals of these

taxa was often detected within the same habitat in different months, resulting in large variation in their densities among tows (as indicated by large SD around their mean values).

In general terms, the grouping of zooplankton assemblages between vegetated and unvegetated habitats in LLT was not as conspicuous as that in LFN in each sampling month (Figure 2.20), though some differences between habitats could still be detected in Mar07, Sep07, Nov07 and Jan08. These between-habitat differences were further revealed by clustering into two groups of samples mainly from the vegetated vs. the unvegetated habitats, at a similarity level of about 50% (Figure 2.21). The major discriminating taxa between habitats were the gammaridean juvenile, the gammaridean of family Synopiidae, the calanoids *Acartia erythrae* and *Pseudodiaptomus incisus* and the harpacticoids. Figure 2.22 shows the population dynamics of these differentiating taxa, which were generally more plentiful in the vegetated than in the unvegetated habitat across the sampling period. Significant difference in abundance between habitats were detected in certain months for some taxa, e.g. *Acartia erythrae* in Sep07 (Mann-Whitney test: $p<0.05$), *Pseudodiaptomus incisus* in Sep07 and Nov07 (Mann-Whitney test: $p<0.05$), harpacticoids in Mar07 and Nov07 (*t*-test: $p<0.05$) and gammaridean amphipod in Mar07 and Jan08 (*t*-test:

$p<0.05$).

On the whole, the more pronounced differences in zooplankton community structure between vegetated and unvegetated habitats were discerned at periods which correspond to the rapid growth (from September to November) and reproductive (from December to January) stages of the major component of the seaweed bed, *Sargassum siliquastrum*, in both sites. The effect of *Sargassum* vegetation on zooplankton abundance and species composition was thus further assessed independently across the sampling period.

2.3.2.2 Comparison between Vegetated and Unvegetated Habitats in terms of Zooplankton Abundance

In LFN, during the early span of the sampling period from Nov06 to Jun07, unvegetated habitat was found to support approximately 3-fold of zooplankton density than that in vegetated habitat (Figure 2.13). However, local variation in zooplankton densities was high and a statistically significant difference in zooplankton abundance between habitats was detected only in Jan07 (t-test: df=4, $p<0.05$). At later dates since Sep07, higher zooplankton densities were encountered in vegetated habitat, with an

8-fold difference observed in Sep07 (Figure 2.13). In LLT, generally, the zooplankton density was higher in vegetated habitat throughout the sampling period, with a statistically significant 4-fold difference (t-test: df= 4, $p<0.05$) recorded in Mar07 and a 3-fold difference recorded in Jun07 (Figure 2.14).

In the main, zooplankton were more abundant in both vegetated and unvegetated habitats in LLT than in LFN. On average, zooplankton density in both vegetated and unvegetated habitats in LLT was about 2-fold more than that in LFN. In spite of this, however, the between-site difference in zooplankton density, either from vegetated or unvegetated habitat, was not statistically significant (t-test and Mann-Whitney test: $p>0.05$, df= 40).

2.3.2.3 Comparison between Vegetated and Unvegetated Habitats in terms of Zooplankton Species Composition

In LFN, the mean zooplankton species richness in the vegetated habitat was in the main greater than that in the unvegetated habitat, except for the period between Mar07 to Sep07. In Nov07, there was a significant difference in species richness between habitats (t-test: df= 4, $p<0.05$), with the vegetated habitat supporting two-time more

species (Figure 2.15 A). The value of Shannon Weaver Diversity Index (H') was, on average, higher in vegetated habitat and significant between-habitat differences were detected in Jan07, Sep07 and Nov07 (t-test: df=4, $p<0.05$). The value of Evenness Index J was also generally higher in vegetated habitat, except in Sep07, and significant between-habitat differences were detected in Jan07, Sep07 and Jan08 (t-test: df= 4, $p<0.05$) (Figure 2.16 A & B). A total of 32 out of 57 taxa (species and groups) were shared by both habitats, while 47 taxa were encountered only in vegetated habitat whereas 42 were recorded only in unvegetated habitat (Table 2.1). The species composition in vegetated habitat was relatively more complex when compared with that in unvegetated habitat across the sampling period (Figure 2.23). The dominant groups of associated zooplankton in the vegetated environment (Figure 2.23 A) were the calanoid copepod, accounting for up to 70- 99% of the total zooplankton population in Jun07-Nov07; the mysid juvenile, contributing up to 15-40% of the assemblage in Nov06, Mar07 and Jan08; and the Gammaridean amphipod that made up 15% of the total population in Jan07. Certain zooplankton could be found more abundantly or only in specific times, e.g. the gammaridean (Nov06-Jun07), the gammaridean juvenile (Jan07-Mar07, Nov07-Jan08), the caprellidean (Jan07-Mar07), the cyclopoid copepod (Jan07 and Jan08), the harpacticoids (Jan07 and Jan08), the fish larvae and eggs (Jun07 and Nov07), the

Isopods (Nov06-Jan07, Nov07-Jan08), the macruran larvae (Nov06-Jan07, Nov07-Jan08), the mysids (Nov06-Mar07), the Lophogaster (Nov07), the squid juvenile (Mar07), the gastropod larvae (Nov06-Jun07) and the molluscan larvae (Mar07). The time occurrence and the density of these zooplankton taxa recorded are given in Table 2.1. On the other hand, in the unvegetated habitat, the most common group was consistently the calanoid copepod throughout the sampling period, accounting for up to 65 - 90% of the total population, and the mysid juvenile, contributing up to 20-80% of the assemblage from Nov06 to Mar07 (Figure 2.23 B). Some groups were found in greater number or only in certain months, e.g. the cyclopoid (Nov06-Jan07), the fish larvae and eggs (Mar07-Sep07), the macruran larvae (Mar07-Sep07), the mysid (Nov06-Mar07), the sergestid (Nov06, Nov07), the arrow worm (Jan08) and the copepod nauplii (Sep07). The time occurrence and the density of these zooplankton groups are also listed in Table 2.1. Figure 2.24 displays the association degree of common zooplankton groups with vegetated and unvegetated habitats in LFN. During the sampling period, the harpacticoid, squid juvenile, molluscan and echinoderm larvae were 100% associated with the *Sargassum siiliquastrum* bed. On the whole, gammaridean amphipod, gammaridean juvenile, caprellidean, isopod, mysid, mysid juveniles and gastropod larvae were mostly associated with the seaweeds. In contrast, hyperiidean, calanoid copepod, sergestids

and arrow worms were generally associated with the unvegetated patch. Some zooplankton groups were alternately associated with vegetation and unvegetated patches from time to time. Brachyuran larvae were totally associated with the vegetation only from Sep07 to Nov07 while alternatively associated with the two habitats in other times. Cyclopoid copepods were wholly associated with the seaweeds from Nov07 to Jan08 but were found in both habitats during the rest of the period. Fish juvenile and eggs were 100% associated with the vegetation from Nov07 to Jan08 but not in the other times. Macruran larvae were completely associated with the seaweeds in Nov06, Jan07, Nov07 and Jan08, but with the unvegetated habitat from Jun to Sep07. *Lophogaster pacificus* were entirely associated with the vegetation from Nov07 to Jan08 but alternatively associated with the two habitats in other times. Polychaetes were 100% associated with vegetated habitat in Jan08 but with unvegetated habitat in Nov07. The copepod nauplii were only encountered in vegetated habitat in Jan08 but were found in unvegetated environment in Nov07.

In LLT, the zooplankton species richness in the vegetated habitat was higher than in the unvegetated habitat over the sampling period. Significant variation in species richness between habitats were obtained (t-test: df= 4, $p<0.05$), with vegetated habitat supporting around 2 times more species in Mar07 and 1.5 times more in Nov07

(Figure 2.15 B). The value of H' was, on average, higher in vegetated habitat and significant between-habitat differences were obtained in Sep07 (t-test: df= 4, $p<0.05$). The value of J was also generally higher in vegetated habitat. In Mar07, J was significantly higher in unvegetated patch (t-test: df= 4, $p<0.05$) while J was significantly greater in vegetated habitat in Sep 07 (t-test: df= 4, $p<0.05$) (Figure 2.16 C & D). A total of 39 out of 63 taxa (species and groups) were shared by both habitats, while 54 were only encountered in vegetated habitat whereas 48 in unvegetated habitat (Table 2.2). The species composition in vegetated habitat was relatively more complex than that in unvegetated environment across the sampling period (Figure 2.25). The prevailing groups of associated zooplankton in the vegetated environment (Figure 2.25 A) were the calanoid copepod, accounting for up to 22- 93% of the total population throughout the sampling time, and the gammaridean juveniles, contributing up to 53% of the total population in Mar07. Some zooplankton groups could be found more abundantly or even only in particular times, e.g. the gammaridean (Jan07-Mar07 and Jan08), the gammaridean juvenile (Jan07-Mar07 and Sep07-Jan08), the caprellidean (Mar07 and Jan08), the cyclopoid copepod (Mar07 and Jan08), the harpacticoids (Mar07 and Jan08), the fish juvenile and eggs (Nov06-Jan07 and Sep07), the isopods (Jan07 and Sep07), the macruran larvae (Nov06-Jan07 and Jan08), the mysids (Jan07 and Sep07), the Lophogasters (Jan07

and Sep07), the squid juvenile (Mar07), the gastropod larvae (Mar07 and Jan08), the molluscan larvae (Mar07) and the echinoderm larvae (Sep07). The time occurrence and density of these zooplankton taxa are illustrated in Table 2.2. In contrast, throughout the sampling period in the unvegetated habitat, the most common group was consistently the calanoid copepod, accounting up to 50 - 80% of the total population (Figure 2.25 B). Some taxa were more abundant or were only found in certain months, e.g. the gammaridean juvenile (Mar07), the cyclopoid (Jan07-Mar07), the fish juvenile and eggs (Jan07-Jun07), the mysid (Jan07), the mysid juvenile (Jan07-Mar07 and Sep07), the sergestid (Nov06 and Nov07), the echinoderm larvae (Sep07), the arrow worm (Nov06 and Mar07) and the copepod nauplii (Jan08). The time occurrence and the density of these zooplankton groups are also listed in Table 2.2. Figure 2.26 displays the association degree of common zooplankton groups with vegetated and unvegetated habitats in LLT. Throughout the sampling period, the isopod, *Lophogaster pacificus* and squid juvenile were entirely associated with the *Sargassum siiliquastrum* bed. In the main, gammaridean amphipod, gammaridean juvenile, caprellidean, harpacticoid, macruran larvae, mysid, mysid juveniles, gastropod larvae, molluscan and echinoderm larvae were mostly associated with the seaweeds. On the other hand, hyperiidean, brachyuran larvae, calanoid copepod and arrow worms were mainly associated with the unvegetated patch. Some zooplankton

taxa were variedly associated with vegetation and unvegetated environments from time to time. Cyclopoid copepods were mostly associated with vegetated habitat in Mar07-Jun07 and Nov07-Jan08 but totally associated with unvegetated patch in Jan07. Fish juvenile and eggs were 100% associated with the seaweed bed in Nov07 while alternatively associated with the two habitats in other times. Sergestids were wholly associated with the vegetation in Mar07 and Sep07 but became mostly associated with the unvegetated environment in the rest of the times. Polychaetes were totally associated with the vegetated habitat in Mar07, Jun07 and Nov07 and shifted their association with the two habitats in other times. The copepod nauplii were 100% associated with vegetation in Jun07 but became associated with the unvegetated patch in Sep07 and Jan08.

When comparing LFN and LLT in terms of their species richness, a significant difference was detected (Mann-Whitney: $p<0.05$, N= 41) in vegetated habitat but not in unvegetated habitat. However, when comparing their H' and J, no significant between-site differences were obtained.

2.3.3 Temporal Trends of Environmental Factors and their Relationship with Zooplankton Assemblage

Figure 2.27 reveals the temporal trend of mean (± S.D.) surface temperature, dissolved oxygen level and salinity in LFN and LLT. In LFN (Figure 2.27 A), the water temperature initially dropped to a level at about 19 ℃ from Nov06 to Jan07. It remained relatively constant during Jan07 to Mar07 and then rose to the maximum at 30.47 ± 0.06 ℃ in Jul07. A gradual decline followed thereafter and hit its minimum at 13.43 ± 0.06 ℃ in Feb08. The mean (± S.D.) dissolved oxygen and salinity levels did not vary as large a magnitude as that observed for temperature. The dissolved oxygen level ranged from 4.15 ± 0.27 mg/L to 8.90 ± 0.28 mg/L. It stayed at a relatively high value over 6 mg/L from Dec06 to Mar07, and diminished to a stable level at about 4 mg/L till Oct07, coinciding with the period with the highest water temperatures. It returned to a high level again starting from Nov07. The salinity level remained comparatively constant at around 32 ppt, except for a sudden plunge to 25.70 ± 0.44 ppt in Jun07. In LLT (Figure 2.27 B), the mean (± S.D.) water temperature increased from 17.27 ± 0.06 ℃ to the maximum at 30.40 ± 0.00 ℃ in Jun07. A steady fall followed in Jul07 and hit its minimum at 13.73 ± 0.06 ℃ in Feb08. The mean (± S.D.) dissolved oxygen level varied from 4.78 ± 0.06 mg/L in Oct07 to 7.17 ± 0.06 mg/L in

Jan07. The salinity level remained relatively stable at about 32 ppt, except for a sudden drop to 24.60 ± 0.00 ppt in Jun07.

Both the zooplankton abundance and species diversity H' did not vary statistically significantly with temperature (Figure 2.28), dissolved oxygen level (Figure 2.29) nor with salinity (Figure 2.30). Zooplankton abundance generally increased, while H' declined with increase in temperature (Figure 2.28). On the other hand, zooplankton abundance dropped whereas H' increased with increase in salinity (Figure 2.30). No general consistent trend between zooplankton assemblage structure and dissolved oxygen level was observed (Figure 2.29).

2.3.4 Relationship between Zooplankton Assemblage and Seaweed Phenology

In LFN, the seaweed (mainly *Sargasssum siliquastrum*) mean (± S.D.) density initially dropped from 76.50 ± 10.35 ind. m^{-2} in Nov06 to 38.50 ± 10.53 ind. m^{-2} in Jan07 (Figure 2.31). A gradual increase was then recorded and the maximum of 102.50 ± 38.30 ind. m^{-2} was attained in Jul07. The density subsequently fell and reached a low level at a range of 30.00 ± 12.28 to 68.50 ± 114.93 ind. m^{-2} from Aug07 to Feb08. In LLT, the seaweed density also first decreased from 69.50 ± 19.24 ind. m^{-2}

in Nov06 to 44.40 ± 20.14 ind. m^{-2} in Mar07. A sharp increase to the maximum of 81.50 ± 17.94 ind. m^{-2} was observed in Apr07. The density then declined steadily and reached its minimum at 23.00 ± 5.55 ind. m^{-2} in Feb08. Between-site difference in seaweed density was detected (Friedman test: df=2, $p<0.05$). In general, the seaweed density in LFN was significantly higher when compared with that in LLT. Zooplankton abundance, Shannon diversity index (H') and Species Evenness index (J) were weakly related with the seaweed density in both sites, but the relationship was statistically not significant (Figure 2.32).

Apart from seaweed density, seaweed length was another seaweed structure investigated for its relationship with the zooplankton assemblage. Significant difference in mean seaweed length (Friedman test: df=2, $p<0.05$) among sites from Nov06 to Jun07 was detected (Figure 2.33). From Nov06 to Jun07, seaweed length in both LFN and LLT fluctuated in a similar manner. The length increased during Nov06 to Jan07 and attained its greatest value in Feb07 at 112.31 ± 49.05 cm in LFN and 104.42 ± 51.80 cm in LLT. The value then fell gradually and reached its lowest at 11.91 ± 7.28 cm in May07 at LFN and 26.45 ± 11.37 cm in Jun07 at LLT. The length of *Sargassum siliquastrum* was on average greater in LFN from Nov06 to Feb07 but lesser from Mar07 to Jun07 when compared with those in LLT, though no significant

between-site difference was detected. Zooplankton abundance was only insignificantly weakly related with seaweed length. However, its Shannon diversity index (H') as well as Species Evenness index (J) were significantly positively related with the seaweed length: H' and J increased with increase in seaweed length (Figure 2.34).

2.4 Discussion

2.4.1 Macro-distribution Pattern and Temporal Change in Zooplankton Assemblage Structure in *Sargassum siliquastrum* Bed

At a regional scale, similarity or differences in zooplankton abundance and species distribution are affected by movement of water masses due to regional hydrographic conditions and local topographical characteristics (Gislason and Astthorsson 2004). Similar population assemblages would co-exist in water bodies which are similar to each other in physical-chemical properties and which experience regular seasonal variation. Therefore, there is spatial homogeneity between structures of the water mass and the zooplankton community (Chen 1992). The similar between-site or between habitats zooplankton assemblage structure in terms of abundance and species

composition over time shown in this study indicates any differences in zooplankton assemblage structure due to local topography of the two study sites or habitats could be over-turned by water masses brought about by the seasonal monsoon climate and its associated greater hydrological environment.

Hong Kong is located in the low-latitudinal subtropical zone, where the zooplankton assemblage structures have no obvious seasonal alternation and peak breeding pattern, with relatively low biomass but high diversity (Chen 1992, Stiling 2002). In this present study, a total density of 1503 ind. m^{-3} (mean density: 71.58 ± 57.97 ind. m^{-3}) were identified in vegetated habitat while 1354 (mean: 64.47 ± 39.60) in unvegetated habitat in LFN. In LLT, a total density of 3167 ind. m^{-3} (mean density: 150.79 ± 155.40 ind. m^{-3}) were collected in vegetated habitat while 2148 (mean: 102.28 ± 39.33) in unvegetated habitat. As the mesh size of the net used in this study was 335 μm, zooplankton density recorded should represent only those zooplankters greater than 335 μm in size. Nevertheless, the abundance recorded in this study was comparable or even higher than those previously reported in other areas. Alldredge and King (1977) reported a density of 2,510 zooplankton m^{-3} emerging from coral reef at Lizard Island Lagoon in the Great Barrier Reef, Australia. Vandendriessche *et al.* (2006) recorded a mean density of 404 m^{-2} of zooplankton larger than 300μm in

size in the floating clumps of seaweeds in Belgian coastal waters. However, meaningful comparisons in zooplankton density are potentially limited by differences in their species composition and the methodology employed, such as mesh sizes of the net used, sampling time and region examined.

In this current study, zooplankton were relatively more abundant from March to September and November 2007. The peaks in abundance during early spring to autumn periods were principally due to the occurrence of dominant zooplankton groups like the calanoids *Acartia erythrae*, *Temora turbinata*, *Pseudodiaptomus incisus*, *Paracalanus parvus* and *Subeucalanus subcrassus*, the mysid juvenile and the gammaridean amphipod. This phenomenon is consistent with previous findings by Chen (1992) in which the high biomass of zooplankton in the northern South China Sea during early spring to autumn periods was mainly caused by the dominant calanoid copepod species. Moreover, Chen (1980), Wong *et al.* (1993) and Lee (2002) reported that *Acartia erythrae, Temora turbinate* and *Subeucalanus subcrassus* were abundant species during the summer to autumn period, while *Paracalanus parvus* and *Undinula vulgaris* were dominant during winter and early spring in northeastern waters of Hong Kong. Seasonal variation in abundance and species composition were mainly brought about by the prevailing monsoons and discharge from the Pearl River.

(Chen 1980, 1992, Lee and Chen 2003, Gislason and Astthorsson 2004). The occurrence of peak abundances might be caused by two probable reasons: seasonal availability of food and breeding periods. Phytoplankton, e.g. the diatoms *Thalassiosira, Chaetoceros, Skeletonema* and some *Coscinodiscus*, were particularly abundant in early spring to early autumn (Chen 1980, Lam and Ho 1989, Yin 2002, Huang *et al.* 2004). The occurrence of high phytoplankton production (Nixon 1988, Ware and Thomson 2005, Frank *et al.* 2006) was due to the influx of nutrients (Chau and Wong 1960, Chau 1962, Watts 1973, Chiu *et al.* 1985) that came with the increased runoff from the Pearl River during wet season from April to September. Therefore, the proliferation of phytoplankton gives rise to the blooming of the calanoid copepods as they filter feed on phytoplankton (Yang and Suen 2006). In addition to the seasonality in food availability, the mysids and the gammaridean undergo synchronized reproduction during early spring to summer (Liu and Wang 2000, Ren 2006, Yang and Suen 2006) and hence contribute to an enormous amount of mysid and gammaridean juveniles in the zooplankton assemblage. All these could contribute to the comparatively high abundance of zooplankton in March to September and in November.

In contrast to zooplankton abundance, zooplankton species richness attained its high value from January to March 2007 and in November 2007 in this present study. This is largely due to the peak abundance of the dominant group, the calanoid copepods during winter and early spring periods in which they were most numerous in terms of their species richness among the zooplankton groups (Chen 1980, Wong *et al.* 1993 and Lee 2002). The relatively low species richness in summer times was likely due to rapid changes in salinity brought about by the increased runoff from the Pearl River Delta as well as local heavy rainfall, resulting in mortality of some species and the prime dominance of those coastal species that can adapt to low salinity, e.g. *Acartia erythrae* (Chen 1992, Wong *et al.* 1993).

Inter-annual variability in zooplankton community structure, due probably to changes in the water mass volume, was reported worldwide (Franks *et al.* 1986, Edwards 2001, Dowd *et al.* 2004, Pershing *et al.* 2005). In this study, zooplankton assemblages also varied significantly among the sampling months, with inter-annual disparity observed in both vegetated and unvegetated habitats. The temporal variation in zooplankton assemblage is largely due to significant difference in zooplankton species richness but not in their abundance.

2.4.2 Effects of Vegetation on the Micro-distribution of Zooplankton within and between Habitats – Relationship between *Sargassum* Phenology and the associated Zooplankton Assemblage Structure

At a micro-scale, patchiness was observed in zooplankton distribution over different substrata in Puerto Rico (Jara 2005) and in the Great Barrier Reef (Alldredge and King 1977). Patchy distribution of zooplankton was also noted in this study as evidenced by the high variation, hence relatively high standard deviation of mean zooplankton abundance in both study sites. Biotic mechanisms, such as trophic interactions of feeding and predation (Newsbury 1972, Omori and Hamner 1982) and synchronized reproduction (Owen 1989, Lonsdale *et al.* 1998), contribute to the formation of zooplankton spatial heterogeneities. In addition to biotic factors, abiotic parameters, e.g. temperature, have been noted for their direct correlation with zooplankton abundance and micro-distribution in upper water layers in the Black and Ionian Seas (Cassie 1963, Tokarev *et al.* 1999). Variability in spatial distribution of plankton can remarkably affect patterns of organic matter and energy transformation in the ecosystem (Davis *et al.* 1991, Tokarev *et al.* 1999), as well as the spatial distribution of planktivores, like fishes, relying on zooplankton as food source (Chen 1980, Alheit 1981, Bullard and Hay 2002, Freseriksen *et al.* 2006).

The relatively higher evenness (J) value in vegetated than in unvegetated habitats suggests a more even distribution in terms of species and the number of individuals in each species in the seaweed bed of *Sargassum siliquastrum* when compared with that in the more open environment of the unvegetated habitat. This might be due to the provision of a variety of heterogeneous microhabitats by the vegetation, thus potentially creating shelters for more zooplankton species and individuals. Moreover, vegetation can dampen the water current (Ekman 1983, Jackson 1985, Eckman *et al.* 1989, Ackerman and Okubo 1993, Johnson and Koehl 1994, Danovaro and Fraschetti 2002, Pakhomov *et al.* 2002). Hydrological environment within the vegetated habitat is more stable, enabling more zooplankton individuals to stay within the habitat.

Sargassum populations have a seasonal cycle of growth, reproduction, senescence and die-back (De Wreede 1976, Ang 1985, Ang 2006). According to Chan (2002), Ang (2006) and Yeung (2009), the *Sargassum siliquastrum* populations in Hong Kong waters exhibited a seasonal cycle of slow growth stage from March to August, rapid growth stage from September to November, reproductive stage from December to January and die-back stage starting in January to February. This present study showed that the zooplankton assemblage structure associated with these seaweed beds was distinctly different from that in unvegetated habitat at certain times of the year

corresponding to the period of rapid growth, reproductive and dieback stages of *Sargassum siliquastrum*, the main canopy species of the seaweed bed in both study sites. In terms of both abundance and species richness, zooplankton were considerably more numerous in vegetated habitat, especially during rapid growth and reproduction of *Sargassum siliquastrum*. This is the period when more complex structure of dense canopy of *Sargassum siliquastrum* is developed (De Wreede 1976, Ang 1985, 2006). Enhanced substratum heterogeneity has been shown to promote higher densities and species richness of zooplankton (Alldredge and King 1977, Porter *et al.* 1977, Kingsford and Choat 1985, Stoner and Lewis 1985, Jacoby and Greenwood 1988, 1989, Kingsford 1992, Shaffer *et al.* 1995, Ingolfsson 1998, Kokita and Omori 1998, Pakhomov *et al.* 2002, Jara 2005, Vandendriessche *et al.* 2006). The complex structure provided by the vegetation, leading to greater abundance and species diversity of zooplankton, may also provide increased food supply (Pakhomov *et al.* 2002), decreased water flow (Ekman 1983, Jackson 1985, Eckman *et al.* 1989, Ackerman and Okubo 1993, Johnson and Koehl 1994, Danovaro and Fraschetti 2002, Pakhomov *et al.* 2002, Thistle 2003), or protection from predators (Thistle *et al.* 1984, Leber 1985, Bullard and Hay 2002). Therefore, algal-bed seasonality could affect the life cycles of its associated fauna (Godoy and Coutinho 2002, King and Sheridan 2006). In this present study, the population dynamics of differentiating species

between habitats varied with seaweed seasonality. During rapid growth, reproductive and dieback stages of *Sargassum siliquastrum*, the gammaridean, the mysid juvenile, the calanoid *Pseudodiaptomus incisus* and the harpacticoids exhibited significantly higher abundance in vegetated environment. The correlation between zooplankton community and seaweed phenology was further verified by the significant positive relation of zooplankton Shannon diversity index H' and Evenness index J with the seaweed length. The effect of vegetation on species richness was more explicit than that on zooplankton abundance. This probably contributed to the distinct difference in zooplankton assemblage structure between vegetated and unvegetated habitats. In short, the tight relationship between zooplankton species richness and seaweed length might be due to the increase in the abundance and type of food items, e.g. epiphytes like filamentous algae, diatoms and bacteria growing on the seaweeds, as well as the host seaweeds themselves, which varies seasonally with the the macroalgal phenology (Huang *et al.* 1989, 1997, 2004, Wong *et al.* 1990, Fu *et al.* 1995, Yin *et al.* 1995, Gasol *et al.* 1997, Martinez- Corfova *et al.* 1998, Calbet 2001, Danovaro and Fraschetti 2002, Coman *et al.* 2003, Ware and Thomson 2005, Martin *et al.* 2006). In addition to the effect of seaweed phenology, other biological factors, such as behavior, trophic interactions and predation among the zooplankton, may be important in structuring the zooplankton communities (Newsbury 1972, Omori and Hamner 1982,

Thistle *et al.* 1984, Leber 1985, Owen 1989, Ashjian and Wishner 1993, Bullard and Hay 2002, Gislason and Astthorsson 2004). These factors have not been investigated in the present study.

The current data suggested that the structure of the zooplankton assemblage in the seaweed bed was only insignificantly weakly influenced by environmental parameters, such as temperature, salinity and dissolved oxygen level. Coman *et al.* (2003) also found that changes in abundance and biomass of the zooplankton assemblage were not correlated with physico-chemical characteristics, e.g. temperature, salinity, dissolved oxygen level and pH, in a commercial shrimp pond in subtropical Australia. It can be surmised that the effect of vegetation on zooplankton assemblage structure was more influential than these abiotic factors examined.

2.4.3 Species Composition of Zooplankton Assemblage in Seaweed Bed of *Sargassum siliquastrum* and its Potential Role as Nursery Ground for Fishery Resources

Substratum preference and biotic mechanisms, such as feeding mode and trophic interaction, might explain the strict linkage of zooplankton species with specific

substratum. Jara (2005) reported that most taxa, including the copepods *Paracalanus* spp., *Pseudodiaptomus* spp. and *Oithona* spp.; amphipods, isopods, and mysis among others were predominantly found associated with more complex substrata (i.e. seagrass and/or sand plus macroalgae). Some groups, namely the calanoid *Acartia* spp., copepod nauplii, cirriped and fish larvae, were collected more frequently over simple substratum (i.e. mud) in tropical Puerto Rico. Moreover, the amphipods, isopods and harpacticoid copepods, being grazers and detritus-feeders, directly utilized kelp as a substratum and hence were strictly associated with the kelps (Hicks 1980, Pakhomov *et al.* 2002). In the present study, harpacticoid, squid juvenile and *Lophogaster pacificus* were totally associated with the *Sargassum* seaweed bed; while gammaridean juvenile, caprellidean, isopods, macruran larvae, mysids and their juveniles, gastropod larvae, molluscan and echinoderm larvae were mostly associated with the seaweeds. The tight association of harpacticoids, isopods, gammaridean juvenile, caprellidean and mysids with *Sargassum siliquastrum* was due to their feeding mode and their likely dependence on affluent food supply provided by the seaweeds. Being detritivores, harpacticoids and mysids (Liu and Wang 2000, Coman *et al.* 2003, Yang and Suen 2006) were only present in copious number during the dieback stage of *Sargassum siliquastrum* when substantial amount of detritus was produced from the decaying seaweed. This phenomenon supported the previous

findings that elevated kelp production coupled with high bacterial biomass and production (Delille *et al.* 1997, 2000) could eventually support a substantial detritivorous fauna within the macroalgal bed (Hicks 1980, Moreno and Jara 1984, Duggins *et al.* 1989). As herbivores on algae (Ren 2006, Yang and Suen 2006), isopods, gammaridean and caprellidean were only present in large number during the reproductive and dieback stages of *Sargassum siliquastrum* when the seaweed and its epiphytes were in bloom. Apart from providing ample food supply, *Sargassum siliquastrum* can create shelter for the zooplankton. Macruran larvae and mysidaceans limited emergence to open waters could reduce their vulnerability to visual predators such as the sergestids and arrow worms (Takahashi and Kawaguchi 1997, Coman *et al.* 2003, Xiao 2004, Jara 2005) which prominently inhabited the unvegetated habitat in this study.

Kelp beds could facilitate the retention of invertebrate and fish larvae, thus acting as a repository for invertebrate and blue crab larvae (Jackson 1985, Eckman et al. 1989, Duggins et al. 1990, Ackerman and Okubo 1993, Johnson and Koehl 1994, Balch and Scheibling 2000, Danovaro and Fraschetti 2002, Pakhomov et al. 2002, Epifanio et al. 2003) as well as nursery and feeding grounds for juveniles of many commercially valuable fish species, e.g. rockfish (Shaffer *et al.* 1995, Kokita and Omori 1998,

Bullard and Hay 2002). Ingólfsson and olafsson (1997) reported a close association between the harpacticoid copepod *Parathalestris croni* and the brown alga *Ascophyllum nodosum*, and its utilization of the seaweeds as a nesting site where the nauplii could crawl on the algae during metamorphosis. In the same sense, an emphasis must be stressed on the potential role as nursery ground of the extensive *Sargassum* bed, as inferred by the close association of invertebrate larvae, e.g. gastropod and echinoderm larvae, and squid and fish juveniles, with *Sargassum siliquastrum* in this study. The recruitment of invertebrate larvae was most likely from January to March, which corresponded to the reproductive and dieback stages of *Sargassum siliquastrum* when tremendous amount of plant detritus was produced for the filter feeding gastropod and other molluscan larvae (Chen 1980, Todd *et al.* 1996). The present findings also showed that the egg-carrying calanoid *Pseudodiaptomus incisus* and the Lophogaster *Lophogaster pacificus* were entirely linked with vegetation, further suggesting that the *Sargassum siliquastrum* bed might serve as a nesting site for these organisms.

2.5 Summary and Conclusion

In this study, zooplankton abundance and species richness were relatively higher from January to March, September and November 2007 in both sites. Seasonal variation in abundance and species composition were likely brought about by the prevailing monsoons and discharge from the Pearl River. At a micro-scale, zooplankton assemblage structure in seaweed bed of *Sargassum siliquastrum* was more distinctly different from that in unvegetated habitat especially during rapid growth, reproductive and dieback stages of *Sargassum siliquastrum*. Difference in species richness contributed to the distinct difference in zooplankton assemblage structure between habitats and species composition in vegetated environment was comparatively more complicated. In comparison, zooplankton assemblage, especially its species richness, was more influenced by seaweed phenology, indicated by seaweed length, than by the physical environmental factors. The close association between zooplankton assemblage and seaweed phenology was likely due primarily to the presence of substantial supply of food source, e.g. plant tissue and detritus, especially during times of reproductive and dieback stages of *Sargassum siliquastrum*; and the complex structure offered by the vegetation, in particular the dense canopy, during the rapid growth, reproductive and dieback stages of the seaweed.

The extensive bed of *Sargassum siliquastrum* in the two sites examined in the present study clearly indicated the close association of subtropical seaweed beds with the zooplankton assemblages. The importance of these seaweed beds as a potential nursery and nesting ground for numerous zooplankton species of economic and ecological significance cannot be underestimated. The evidences provided in the present study highlight the conservation values of these seaweed beds. Management strategies for their protection should thus be part of any coastal developmental plan in order to ensure that this complex association is sustained for the future.

Table 2.1 The mean (± S.D.) density (m^{-3}) of different zooplankton taxonomic groups collected in both vegetated and unvegetated habitats in each sampling month in LFN. Shaded taxa were present only in LLT but not in LFN. Some taxa are labeled with trophic modes. Trophic mode abbreviations: f= filter feeder, d= detritus feeder, h= hernivore, o= omnivore, c= carnivore, sv= scavenger, ep= ectoparasite.

Taxonomic groups	Trophic mode	Nov-06		Jan-07		Mar-07		Jun-07		Sep-07		Nov-07		Jan-08	
		vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated
Amphipoda															
Gammaridean	h														
Synopiidae		0.47 ± 0.82	0.24 ± 0.41	4.01 ± 2.16	0.24 ± 0.41	1.18 ± 0.41	0.94 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Maxillipidae		0.24 ± 0.41	0.00 ± 0.00	0.94 ± 1.08	0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Talitridae		0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Stenothoidae		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Gammaridea juvenile		0.00 ± 0.00	0.00 ± 0.00	3.07 ± 2.95	1.42 ± 1.42	1.42 ± 1.42	0.71 ± 0.71	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	1.42 ± 1.42	0.24 ± 0.41
Caprellidean	h	0.00 ± 0.00	0.00 ± 0.00	0.94 ± 0.82	0.47 ± 0.41	1.18 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Hyperiidean	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Decapoda															
Brachyura larva		0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Anomura larva		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Macrura larva		0.24 ± 0.41	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.47 ± 0.82	0.94 ± 1.08	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00
Sergestidae, *Lucifer* spp.	c	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00
Acetes japonica	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.41	0.00 ± 0.00	0.00 ± 0.00
Sergestidae larva		**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Copepoda															
Calanoida	f														
Acartia erythrae		0.47 ± 0.41	0.94 ± 1.08	0.94 ± 1.63	42.93 ± 25.37	0.00 ± 0.00	0.24 ± 0.41	88.46 ± 100.17	155.93 ± 102.32	238.03 ± 244.23	8.73 ± 10.97	2.83 ± 1.87	13.45 ± 14.32	0.47 ± 0.41	12.74 ± 3.68
Temora turbinata		0.71 ± 0.71	0.24 ± 0.41	2.59 ± 1.52	1.18 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.71 ± 0.71	0.71 ± 0.71	2.83 ± 1.87	6.37 ± 2.55	6.61 ± 0.82	0.00 ± 0.00	0.00 ± 0.00
Subeucalanus subcrassus		0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	2.59 ± 2.68
Pseudodiaptomus spp.		0.47 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Pseudodiaptomus incisus		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	5.43 ± 8.38	1.18 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	7.78 ± 3.09	0.71 ± 0.71	0.00 ± 0.00	0.00 ± 0.00
Labidocera minuta		0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.47 ± 0.82	0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Paracalanus parvus		0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.94 ± 1.63	0.24 ± 0.41	4.01 ± 1.08	4.48 ± 4.32	2.59 ± 0.41	12.27 ± 8.20
Paracalanus aculeatus		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Paracalanus spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.89 ± 2.16
Tortanus forcipatus		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.71 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00
Tortanus gracilis		**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Undinula vulgaris		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	1.89 ± 0.82	0.71 ± 0.71	0.24 ± 0.41	0.00 ± 0.00
Euchaeta spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Calanopida elliptica		**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Centropages orsinii		**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Centropages tenuiremis		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.71 ± 0.82
Centropages gracilis		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Centropages calanmus		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41
Cyclopoida	c														
Oithona simplex		0.00 ± 0.00	0.00 ± 0.00	1.42 ± 2.54	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Oithona rigida		0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.71 ± 1.23	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Oithona spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.71 ± 0.71	0.00 ± 0.00
unidentified 1		0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Microsetella norvegica		**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Corycaeus spp.		0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Harpacticoida	d	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.71 ± 0.71	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.41	0.00 ± 0.00	1.42 ± 0.71	0.00 ± 0.00
Poecilostomatoida	ep														
Cymbasoma spp.		**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Copepoda nauplii		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.89 ± 2.16	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

Table 2.1 (cont'd)

Taxonomic groups	Trophic mode	Nov-06		Jan-07		Mar-07		Jun-07		Sep-07		Nov-07		Jan-08	
		vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated
Fish larva															
Synodontidae	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.89 ± 1.47	0.24 ± 0.41	0.71 ± 0.71	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Monacanthidae	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Petroscrites breviceps	o	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00
Sebastiscus marmoratus	**c**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Fish eggs		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	1.42 ± 0.71	0.71 ± 0.71	0.00 ± 0.00	0.47 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Isopoda adult	h	2.12 ± 2.55	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00
Isopoda juvenile		**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Mysidacea															
Mysida	o														
Siriella vulgaris	d, c	0.71 ± 1.23	0.00 ± 0.00	0.71 ± 0.71	0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Unidentified 1		0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	1.42 ± 2.08	3.30 ± 5.72	3.30 ± 3.55	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mysidopsis indica	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Anisomysis ijimai		**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Iiella ohshimai		**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Mysidae juvenile		6.37 ± 5.66	5.19 ± 8.38	4.25 ± 3.74	12.74 ± 6.75	5.43 ± 9.40	94.13 ± 98.95	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.47 ± 0.41	15.81 ± 23.71	0.00 ± 0.00
Lophogastrida															
Lophogaster pacificus	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.18 ± 2.04	0.00 ± 0.00	0.71 ± 0.82	0.00 ± 0.00
Lophogastridae juvenile	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.47 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mollusca															
Squid juvenile	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Gastropoda, *Creseis acicula*	f	0.00 ± 0.00	0.00 ± 0.00	lots	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	lots	0.00 ± 0.00
Gastropoda unidentified larva	f	0.47 ± 0.41	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41	0.47 ± 0.82	0.00 ± 0.00	0.47 ± 0.82	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.71 ± 1.23	0.00 ± 0.00	0.00 ± 0.00
Molluscus, Lamellibrachia larva	f	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.94 ± 1.63	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Echinodermata unidentified larva	f	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Polychaeta larva	c	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00
Chaetognatha															
Sagitta enflata	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	6.61 ± 7.57
Sagitta regularis	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.24 ± 0.41
Cirripedia larva	f	2.36 ± 2.86	1.18 ± 1.47	0.47 ± 0.82	1.42 ± 0.00	21.70 ± 4.15	19.58 ± 11.51	0.94 ± 1.08	0.47 ± 0.82	0.71 ± 0.71	2.36 ± 1.47	4.25 ± 2.12	0.94 ± 1.63	12.50 ± 7.57	4.25 ± 1.42
Cladocera	f	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.24 ± 0.41	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00
Cumacea	**d**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Cnidaria															
Hydroid polyp	c	0.00 ± 0.00	0.00 ± 0.00	0.71 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.24 ± 0.41	0.24 ± 0.41	0.47 ± 0.82	0.24 ± 0.41	0.00 ± 0.00	1.18 ± 1.08	0.71 ± 0.00	11.80 ± 13.25	0.47 ± 0.41
Hydrozoa medusa	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.71 ± 0.71	0.47 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	1.42 ± 1.23
Nemertea	c, sv	0.24 ± 0.41	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Ostracoda	**f or o**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Oikopleura		0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Others, e.g. insecta		0.47 ± 0.82	0.94 ± 1.63	0.00 ± 0.00	0.71 ± 0.71	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00
Total		15.57 ± 12.03	11.09 ± 13.38	20.76 ± 14.30	64.87 ± 21.84	37.51 ± 15.52	119.84 ± 96.70	100.02 ± 95.96	162.30 ± 105.45	242.04 ± 244.83	19.11 ± 14.78	36.57 ± 7.09	30.43 ± 21.80	48.83 ± 14.91	43.64 ± 3.27

Table 2.2 The mean (± S.D.) density (m^{-3}) of different zooplankton groups in both vegetated and unvegetated habitats collected in each sampling month in LLT. Shaded taxa were present only in LLT but not in LFN. Some taxa are labeled with trophic modes. Trophic mode abbreviations: f= filter feeder, d= detritus feeder, h= hernivore, o= omnivore, c= carnivore, sv= scavenger, ep= ectoparasite

Taxonomic groups	Trophic mode	Nov-06		Jan-07		Mar-07		Jun-07		Sep-07		Nov-07		Jan-08	
		vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated
Amphipoda															
Gammaridean	h														
Synopiidae		0.00 ± 0.00	0.00 ± 0.00	2.12 ± 1.50	0.00 ± 0.00	38.45 ± 10.74	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.18 ± 1.47	0.24 ± 0.41	1.89 ± 1.08	0.00 ± 0.00
Maxillipidae		0.24 ± 0.41	0.00 ± 0.00	0.35 ± 0.50	0.00 ± 0.00	0.71 ± 0.71	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Talitridae		0.00 ± 0.00	0.00 ± 0.00	0.35 ± 0.50	0.00 ± 0.00	5.90 ± 3.27	0.94 ± 1.63	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00
Stenothoidae		0.00 ± 0.00	0.00 ± 0.00	0.71 ± 0.00	0.00 ± 0.00	0.47 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Gammaridea juvenile		0.00 ± 0.00	0.00 ± 0.00	1.42 ± 2.00	0.24 ± 0.41	128.80 ± 54.88	3.54 ± 2.55	0.71 ± 0.71	0.00 ± 0.00	0.71 ± 0.71	0.00 ± 0.00	3.07 ± 4.15	0.47 ± 0.82	5.66 ± 3.24	0.24 ± 0.41
Caprellidean	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	1.89 ± 1.47	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.18 ± 2.04	0.00 ± 0.00	0.94 ± 0.41	0.00 ± 0.00
Hyperiidean	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Decapoda															
Brachyura larva		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.47 ± 0.41	0.00 ± 0.00	0.71 ± 0.71	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00
Anomura larva		**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Macrura larva		0.24 ± 0.41	0.71 ± 0.71	1.77 ± 0.50	0.00 ± 0.00	0.47 ± 0.41	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.94 ± 0.82	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41
Sergestidae, *Lucifer* spp.	c	0.47 ± 0.82	5.19 ± 4.71	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	4.48 ± 2.95	104.03 ± 53.09	0.00 ± 0.00	0.00 ± 0.00
Acetes japonica	c	0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.24 ± 0.41	0.47 ± 0.41	0.00 ± 0.00	0.00 ± 0.00
Sergestidae larva		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Copepoda															
Calanoida	f														
Acartia erythrae		5.90 ± 2.86	53.79 ± 57.22	2.12 ± 2.00	12.27 ± 17.17	0.24 ± 0.41	0.00 ± 0.00	360.46 ± 582.35	114.18 ± 18.48	1.89 ± 3.27	53.08 ± 23.93	265.39 ± 377.28	127.15 ± 43.92	0.94 ± 1.08	0.71 ± 1.23
Temora turbinata		10.85 ± 8.53	21.94 ± 22.94	1.77 ± 0.50	0.24 ± 0.41	2.83 ± 1.23	20.29 ± 20.44	1.18 ± 1.08	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.71 ± 0.71	0.71 ± 0.71	0.00 ± 0.00	0.00 ± 0.00
Subeucalanus subcrassus		0.71 ± 1.23	1.42 ± 2.45	0.00 ± 0.00	0.00 ± 0.00	1.42 ± 1.23	0.94 ± 1.08	0.24 ± 0.41	0.94 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	1.89 ± 1.78	2.59 ± 3.36	4.25 ± 1.23
***Pseudodiaptomus* spp.**		**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Pseudodiaptomus incisus		0.71 ± 0.71	2.83 ± 3.74	0.35 ± 0.50	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	1.42 ± 1.23	0.00 ± 0.00	1.18 ± 0.82	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00
Labidocera minuta		0.47 ± 0.41	2.36 ± 3.49	0.00 ± 0.00	0.47 ± 0.82	0.71 ± 1.23	0.71 ± 1.23	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Paracalanus parvus		0.00 ± 0.00	0.00 ± 0.00	9.91 ± 4.00	0.71 ± 0.71	5.19 ± 4.15	5.43 ± 4.02	1.89 ± 0.41	1.89 ± 1.47	0.00 ± 0.00	0.24 ± 0.41	4.95 ± 2.55	6.61 ± 0.41	7.55 ± 7.53	20.29 ± 15.78
Paracalanus aculeatus		0.71 ± 1.23	1.18 ± 2.04	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
***Paracalanus* spp.**		**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Tortanus forcipatus		0.00 ± 0.00	0.94 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Tortanus gracilis		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.71 ± 0.71	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00
Undinula vulgaris		0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.47 ± 0.82	0.71 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.94 ± 1.08	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.41	2.36 ± 2.96	0.00 ± 0.00	0.47 ± 0.41
Euchaeta spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.71 ± 1.23	0.24 ± 0.41
Calanopida elliptica		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Centropages orsinii		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Centropages temuremis		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Centropages gracilis		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	2.83 ± 3.27	0.00 ± 0.00	0.00 ± 0.00
Centropages calanmus		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41
Cyclopoida	c														
Oithona simplex		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	2.59 ± 4.49	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Oithona rigida		**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Oithona spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	3.30 ± 3.56	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
unidentified 1		**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**	**0.00 ± 0.00**
Microsetella norvegica		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Corycaeus spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	2.36 ± 2.16	2.36 ± 2.04	1.18 ± 1.47	0.47 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Harpacticoida	d	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	5.66 ± 1.87	0.47 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	5.43 ± 2.16	0.94 ± 1.63	2.36 ± 2.04	2.83 ± 3.74
Poecilostomatoida	ep														
Cymbasoma spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Copepoda nauplii		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.65 ± 1.78	1.42 ± 1.87	0.47 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.41

Table 2.2 (cont'd)

Taxonomic groups	Trophic mode	Nov-06		Jan-07		Mar-07		Jun-07		Sep-07		Nov-07		Jan-08	
		vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated	vegetated	unvegetated
Fish larva															
Synodontidae	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41	0.47 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Monacanthidae	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Petroscrites breviceps	o	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Sebastiscus marmoratus	c	0.00 ± 0.00	0.00 ± 0.00	0.35 ± 0.50	0.00 ± 0.00	0.71 ± 0.71	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Fish eggs		0.47 ± 0.82	0.24 ± 0.41	0.00 ± 0.00	0.94 ± 1.63	0.94 ± 0.41	0.00 ± 0.00	2.12 ± 2.55	6.84 ± 2.86	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Isopoda adult	h	0.00 ± 0.00	0.00 ± 0.00	0.71 ± 1.00	0.00 ± 0.00	0.47 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00
Isopoda juvenile		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mysidacea															
Mysida	o														
Siriella vulgaris	d, c	0.00 ± 0.00	0.00 ± 0.00	0.35 ± 0.50	0.00 ± 0.00	0.47 ± 0.41	0.00 ± 0.00	1.18 ± 2.04	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Unidentified 1		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mysidopsis indica	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Anisomysis ijimai		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.71 ± 0.71	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Iiella ohshimai		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mysidae juvenile		0.24 ± 0.41	0.00 ± 0.00	0.71 ± 1.00	0.71 ± 1.23	5.43 ± 4.55	1.65 ± 1.47	3.30 ± 4.55	0.24 ± 0.41	0.24 ± 0.41	1.89 ± 1.78	1.89 ± 0.82	0.71 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Lophogastrida															
Lophogaster pacificus	c	0.00 ± 0.00	0.00 ± 0.00	1.42 ± 1.00	0.00 ± 0.00	1.65 ± 1.47	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Lophogastridae juvenile	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mollusca															
Squid juvenile	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Gastropoda, *Creseis acicula*	f	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	5.90 ± 10.21	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	lots	0.00 ± 0.00
Gastropoda unidentified larva	f	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.94 ± 1.08	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.71 ± 0.71	0.24 ± 0.41	0.71 ± 0.71	0.24 ± 0.41
Molluscus, Lamellibrachia larva	f	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.94 ± 1.63	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Echinodermata unidentified larva	f	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.65 ± 2.27	5.90 ± 5.41	2.83 ± 1.87	0.71 ± 1.23	0.00 ± 0.00	0.00 ± 0.00
Polychaeta larva	c	0.47 ± 0.82	2.12 ± 1.87	0.35 ± 0.50	0.47 ± 0.41	1.42 ± 1.87	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.94 ± 1.08	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41
Chaetognatha															
Sagitta enflata	c	0.00 ± 0.00	13.92 ± 17.28	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.42 ± 2.45	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Sagitta regularis	c	0.00 ± 0.00	3.30 ± 5.72	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.71 ± 0.71	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00
Cirripedia larva	f	0.94 ± 1.08	0.00 ± 0.00	8.49 ± 1.00	3.30 ± 1.47	6.61 ± 3.63	3.54 ± 1.87	1.18 ± 1.08	0.71 ± 1.23	4.72 ± 1.63	4.25 ± 1.23	2.36 ± 1.47	4.48 ± 1.08	0.24 ± 0.41	1.65 ± 1.78
Cladocera	f	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.42 ± 1.87	2.59 ± 1.08	14.39 ± 16.14	16.51 ± 19.15	0.71 ± 0.71	1.65 ± 1.63	0.47 ± 0.41	0.47 ± 0.41	0.24 ± 0.41	0.00 ± 0.00
Cumacea	d	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.94 ± 0.82	0.47 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00
Cnidaria															
Hydroid polyp	c	4.95 ± 3.94	0.71 ± 1.23	0.35 ± 0.50	0.24 ± 0.41	1.18 ± 1.47	0.24 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.82	0.94 ± 0.82	4.01 ± 0.82	2.12 ± 1.87	2.36 ± 0.82	0.94 ± 0.82
Hydrozoa medusa	c	0.00 ± 0.00	0.00 ± 0.00	0.35 ± 0.50	0.00 ± 0.00	2.36 ± 0.82	1.18 ± 1.08	0.24 ± 0.41	0.24 ± 0.41	0.00 ± 0.00	0.47 ± 0.41	1.65 ± 1.47	0.00 ± 0.00	0.00 ± 0.00	2.59 ± 2.27
Nemertea	c, sv	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.42 ± 1.42	0.71 ± 0.00	2.59 ± 1.08	0.94 ± 0.41	0.00 ± 0.00	0.00 ± 0.00
Ostracoda	f or o	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.00 ± 0.00
Oikopleura		0.24 ± 0.41	3.07 ± 4.15	0.00 ± 0.00	0.00 ± 0.00	7.78 ± 8.34	9.20 ± 12.91	0.71 ± 0.71	0.71 ± 0.71	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	3.54 ± 2.83
Others, e.g. insecta		0.24 ± 0.41	2.59 ± 4.49	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.41	0.24 ± 0.41	1.42 ± 1.42	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.18 ± 1.47	0.94 ± 1.63
Total		28.07 ± 15.38	117.01 ± 123.64	35.03 ± 11.51	21.00 ± 20.63	244.16 ± 67.73	60.86 ± 44.81	392.55 ± 608.78	147.68 ± 22.67	15.81 ± 4.97	70.30 ± 26.39	310.69 ± 373.94	258.79 ± 23.56	29.25 ± 5.72	40.34 ± 15.52

Table 2.3 Results of SIMPER analysis showing the discriminating taxa among sampling months in vegetated and unvegetated habitats in LFN. Discriminating taxa are those making a large contribution to differences between sampling months, listed in order of decreasing importance.

Vegetated						
	Nov-06	Jan-07	Mar-07	Jun-07	Sep-07	Nov-07
Jan-07	GJ, GS, Ci					
Mar-07	MJ, C, TT	Ci, TT, ML				
Jun-07	MJ, AE, PI	AE, GS, GJ	AE, Ci, C			
Sep-07	MJ, AE, Ci	AE, GS, GJ	AE, Ci, C	FE, PI, TT		
Nov-07	MJ, PP, UV	PI, GS, UV	PI, TT, PP	TT, UV, PP	PI, AE, PP	
Jan-08	HP, PP, H	GS, TT, Ci	HP, MJ, PP	AE, MJ, HP	AE, MJ, HP	PI, TT, MJ
Unvegetated						
	Nov-06	Jan-07	Mar-07	Jun-07	Sep-07	Nov-07
Jan-07	AE, MJ, TT					
Mar-07	Ci, FS, MJ	AE, TT, FS				
Jun-07	AE, MJ, Ci	MJ, Ci, PI	AE, MJ, Ci			
Sep-07	MJ, TT, AE	MJ, CN, FE	MJ, AE, TT	Ci, TT, CN		
Nov-07	PP, MJ, TT	PP, HP, MJ	TT, AE, MJ	PP, TT, HP	Ci, PP, HP	
Jan-08	PP, MJ, SE	MJ, PP, SS	MJ, PP, AE	PP, SS, Ci	TT, PP, SS	TT, SS, SE

[Taxa abbreviations: GJ= Gammaridean juvenile, GS= Gammaridean Synopiidae, C= Caprellidean, AE= *Acartia erythrae*, PI= *Pseudodiaptomus incisus*, PP= *Paracalanus parvus*, SS= *Subeucalanus subcrassus*, TT= *Temora turbinata*, UV= *Undinula vulgaris*, H= Harpacticoida, CN= Copepoda nauplii, MJ= Mysidae juvenile, FE= Fish egg, FS= Fish Synodontidae, Ci= Cirripedia, HP= Hydroid polyp, SE= *Sagitta enflata*]

Table 2.4 Results of SIMPER analysis showing the discriminating taxa among sampling months in vegetated and unvegetated habitats in LLT (n.s.: no significant result). Discriminating taxa are those making a large contribution to differences between sampling months, listed in order of decreasing importance.

Vegetated						
	Nov-06	Jan-07	Mar-07	Jun-07	Sep-07	Nov-07
Jan-07	PP, GS, HP					
Mar-07	GJ, GS, AE	GJ				
Jun-07	HP, TT, PP	GS, LP, ML	AE, GS, GJ			
Sep-07	TT, Ci, AE	PP, GS, ML	GS	AE, PP, Ci		
Nov-07	TT, H	LP, H	AE, GJ	H, SL, HP	AE, Ci	
Jan-08	TT, GJ, PP	Ci, SS, TT	n.s.	AE, HP, GS	PP, Ci, SS	AE, SS
Unvegetated						
	Nov-06	Jan-07	Mar-07	Jun-07	Sep-07	Nov-07
Jan-07	Ci, TT, TF					
Mar-07	AE, Ci, GJ	TT, AE, O				
Jun-07	TT, Cl, TF	Ci, AE, Cl	AE, TT, GJ			
Sep-07	TT, Ci, TF	AE, EL, Cl	AE, TT, O	FE, EL, Ci		
Nov-07	SL, TT, TF	SL, AE, Ci	AE, SL, TT	SL, FE, Cl	SL, EL, PP	
Jan-08	PP, AE, TT	SS, PP, O	TT, Cl, GJ	AE, PP, FE	AE, PP, SS	SL, AE, O

[Taxa abbreviations: GJ= Gammaridean juvenile, GS= Gammaridean Synopiidae, AE= *Acartia erythrae*, PP= *Paracalanus parvus*, SS= *Subeucalanus subcrassus*, TT= *Temora turbinata*, TF= *Tortanus forcipatus*, UV= *Undinula vulgaris*, H= Harpacticoida, CN= Copepoda nauplii, MJ= Mysidae juvenile, LP= *Lophogaster pacificus*, ML= Macrura larva, SL= Sergestidae *Lucifer* spp., FE= Fish egg, Ci= Cirripedia, Cl= Cladocera, EL= Echinodermata larva, O= *Oikopleura*, HP= Hydroid polyp]

Table 2.5 Results of Pairwise ANOSIM comparisons in vegetated habitat between sites in each sampling month (all values, $p<0.05$) and SIMPER analysis showing the discriminating taxa between sites. Discriminating taxa are those making a large contribution to differences between sites in the respective month, listed in order of decreasing importance.

LLT	LFN						
	Pairwise ANOSIM						
	Nov-06	Jan-07	Mar-07	Jun-07	Sep-07	Nov-07	Jan-08
Nov-06	0.926	0.963	1	0.556	0.778	0.667	1
Jan-07	0.667	0.417	1	1	1	0.583	1
Mar-07	1	0.778	1	1	1	1	1
Jun-07	0.889	0.926	1	0.074	0.296	0.741	0.815
Sep-07	0.556	0.926	0.741	0.741	0.889	0.519	0.63
Nov-07	1	0.889	1	0.741	0.963	0.778	1
Jan-08	1	0.815	1	1	1	1	1
SIMPER							
	Nov-06	Jan-07	Mar-07	Jun-07	Sep-07	Nov-07	Jan-08
Nov-06	MJ, HP, TT						
Jan-07		PP, Ci, LP					
Mar-07			GJ, Ci				
Jun-07				PI, PP, Cl			
Sep-07					AE, Ci, PI		
Nov-07						TT, PI	
Jan-08							MJ, Ci, SS

[Taxa abbreviations: GJ= Gammaridean juvenile, AE= *Acartia erythrae*, PP= *Paracalanus parvus*, SS= *Subeucalanus subcrassus*, TT= *Temora turbinata*, MJ= Mysidae juvenile, LP= *Lophogaster pacificus*, Ci= Cirripedia, Cl= Cladocera, HP= Hydroid polyp]

Table 2.6 Results of Pairwise ANOSIM comparisons in unvegetated habitat between sites in each sampling month (all values, $p<0.05$) and SIMPER analysis showing the discriminating taxa between sites. Discriminating taxa are those making a large contribution to differences between sites in the respective month, listed in order of decreasing importance.

		LFN						
	Pairwise ANOSIM							
		Nov-06	Jan-07	Mar-07	Jun-07	Sep-07	Nov-07	Jan-08
	Nov-06	0.426	0.815	1	0.444	0.815	0.481	1
	Jan-07	0.111	0.222	0.519	0.481	0.222	0.333	0.259
	Mar-07	0.352	1	1	1	0.889	0.963	0.963
	Jun-07	0.37	1	1	1	0.741	1	1
	Sep-07	0.352	1	1	1	0.852	1	1
	Nov-07	0.333	1	1	1	0.963	1	1
	Jan-08	0.574	1	1	1	0.926	0.963	0.741
LLT	SIMPER							
		Nov-06	Jan-07	Mar-07	Jun-07	Sep-07	Nov-07	Jan-08
	Nov-06	MJ, AE, TT						
	Jan-07		MJ, AE, Ci					
	Mar-07			TT, MJ, PP				
	Jun-07				Cl, PP, PI			
	Sep-07					TT, EL, CN		
	Nov-07						SL, TT, Ci	
	Jan-08							AE, O, SE

[Taxa abbreviations: AE= *Acartia erythrae*, PI= *Pseudodiaptomus incisus*, PP= *Paracalanus parvus*, TT= *Temora turbinata*, CN= Copepoda nauplii, MJ= Mysidae juvenile, LP= *Lophogaster pacificus*, SL= Sergestidae *Lucifer* spp., Ci= Cirripedia, Cl= Cladocera, EL= Echinodermata larva, O= *Oikopleura*, HP= Hydroid polyp, SE= *Sagitta enflata*]

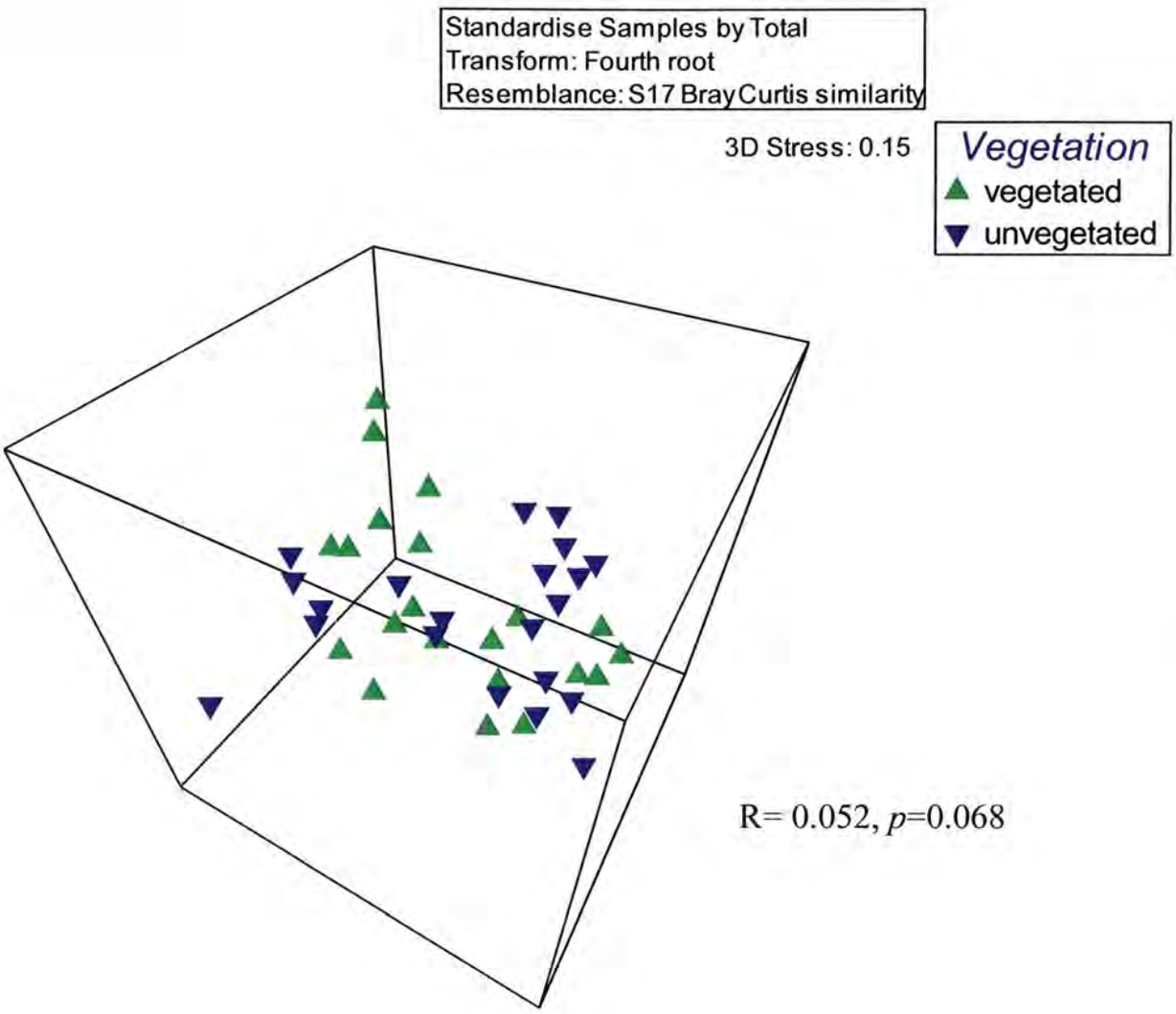


Fig. 2.1 MDS ordination plot showing the structure of zooplankton assemblages between vegetated and unvegetated habitats in LFN (stress = 0.15). Each point represents data for each zooplankton tow over the sampling period from November 06 to January 08. ANOSIM results (with Global-R = 0.052) indicate overlap with no significant differences in the structure of zooplankton assemblages between groups in vegetated and unvegetated habitats.

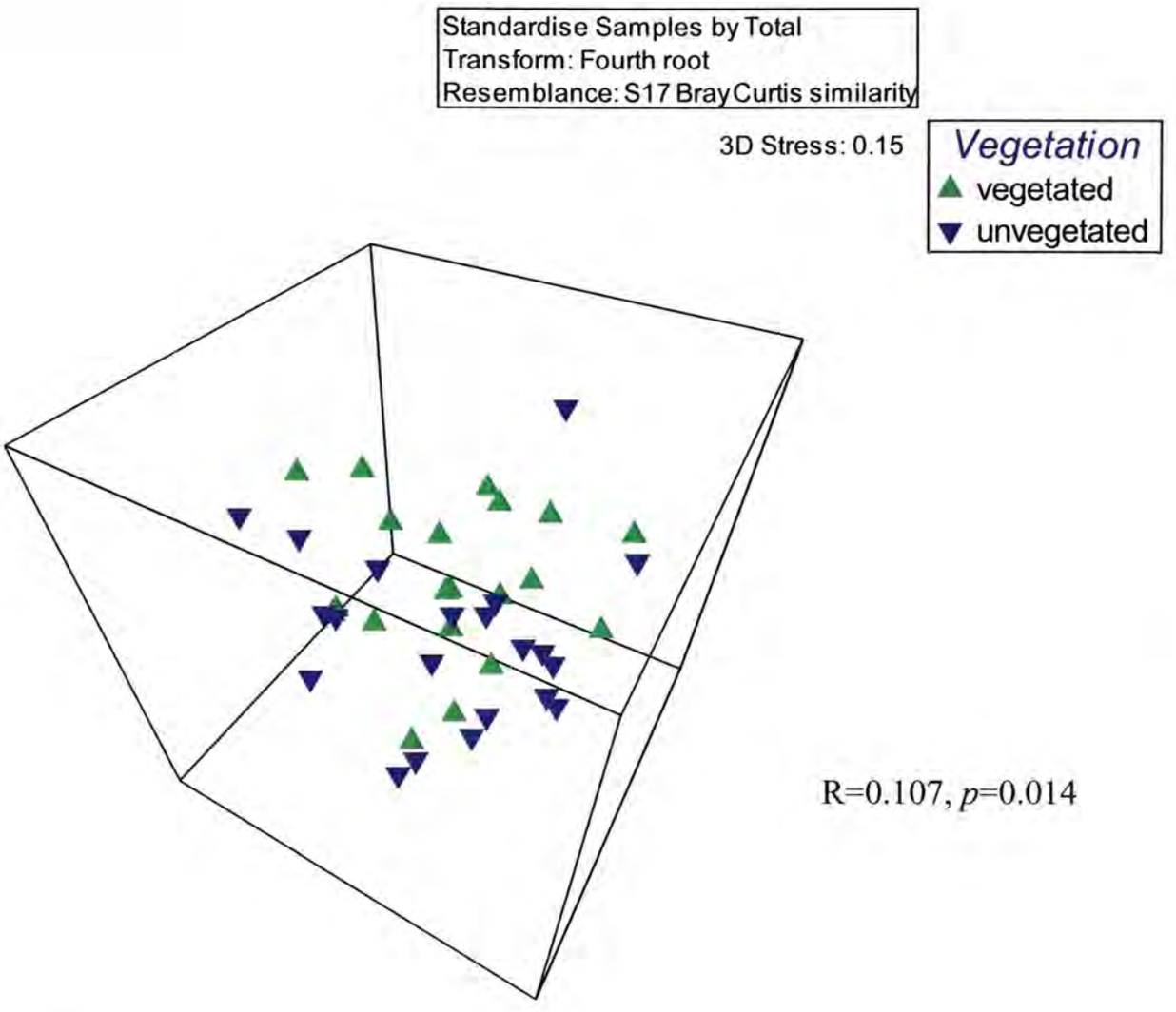


Fig. 2.2 MDS ordination plot showing the structure of zooplankton assemblages between vegetated and unvegetated habitats in LLT (stress = 0.15). Each point represents data for each zooplankton tow over the sampling period from November 06 to January 08. ANOSIM results (with Global-R = 0.107) indicate significant overlapping in the structure of zooplankton assemblages between groups in vegetated and unvegetated habitats.

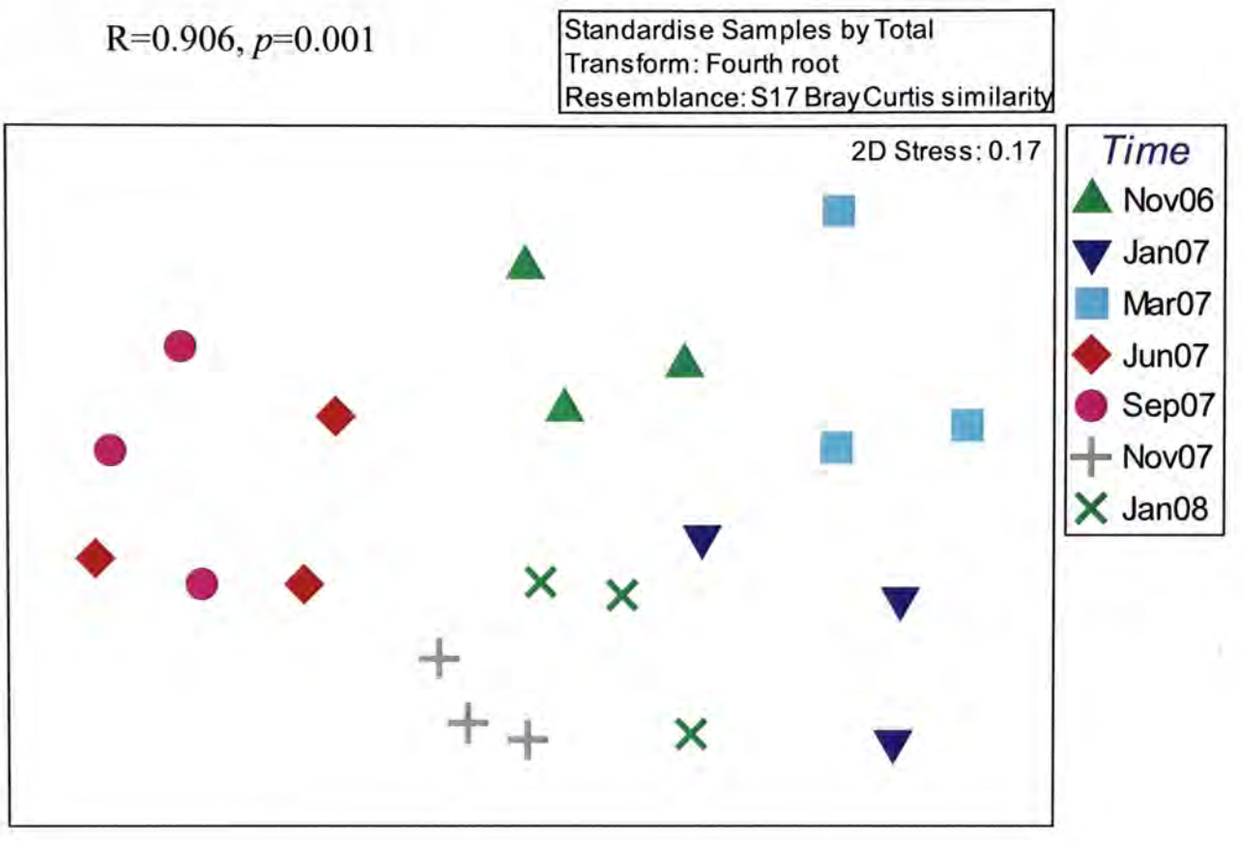


Fig. 2.3 MDS ordination plot showing the structure of zooplankton assemblages among sampling months in vegetated habitat in LFN (Stress = 0.17). Each point represents data for each zooplankton tow in vegetated habitat over the sampling period from November 06 to January 08. ANOSIM results (with Global-R = 0.906) indicate significant separation in the structure of zooplankton assemblages among groups.

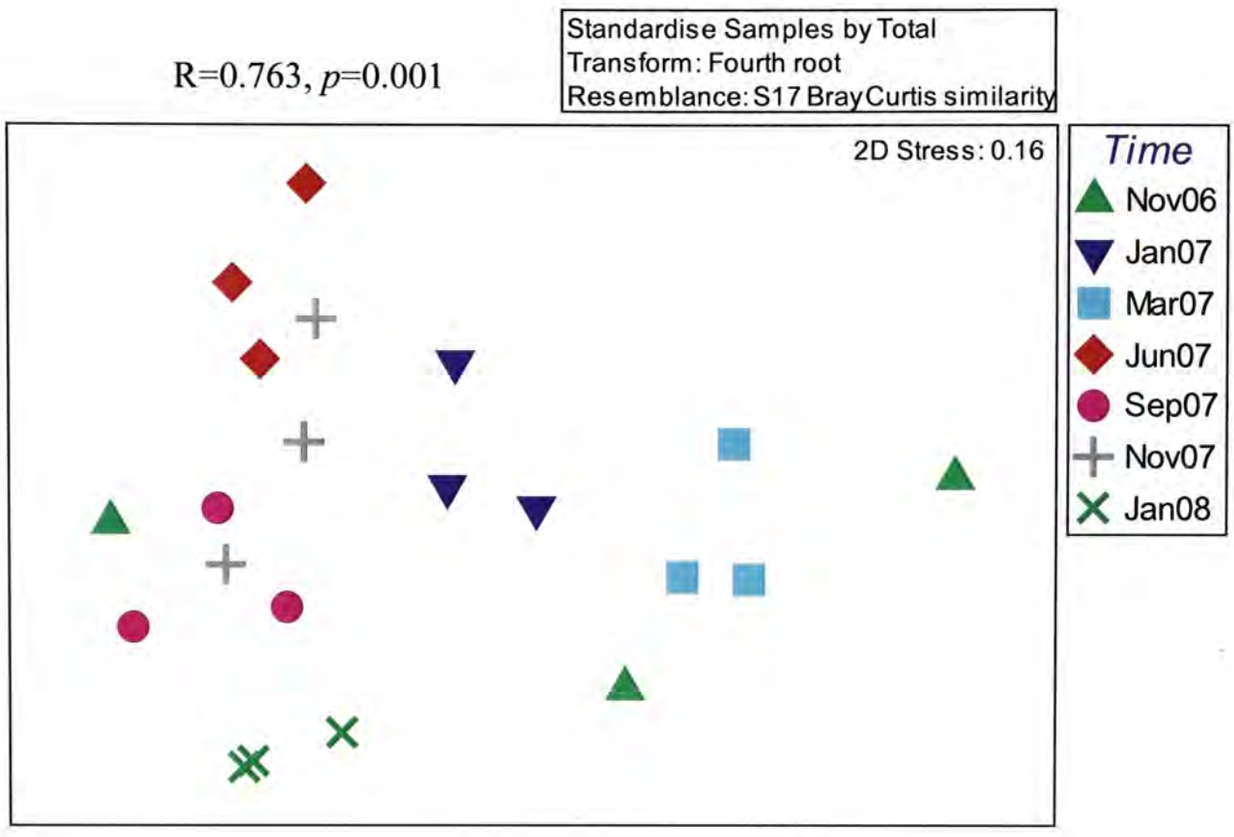


Fig. 2.4 MDS ordination plot showing the structure of zooplankton assemblages among sampling months in unvegetated habitat in LFN (stress = 0.16). Each point represents data for each zooplankton tow in unvegetated habitat over the sampling period from November 06 to January 08. ANOSIM results (with Global-R = 0.763) indicate significant separation in the structure of zooplankton assemblages among groups.

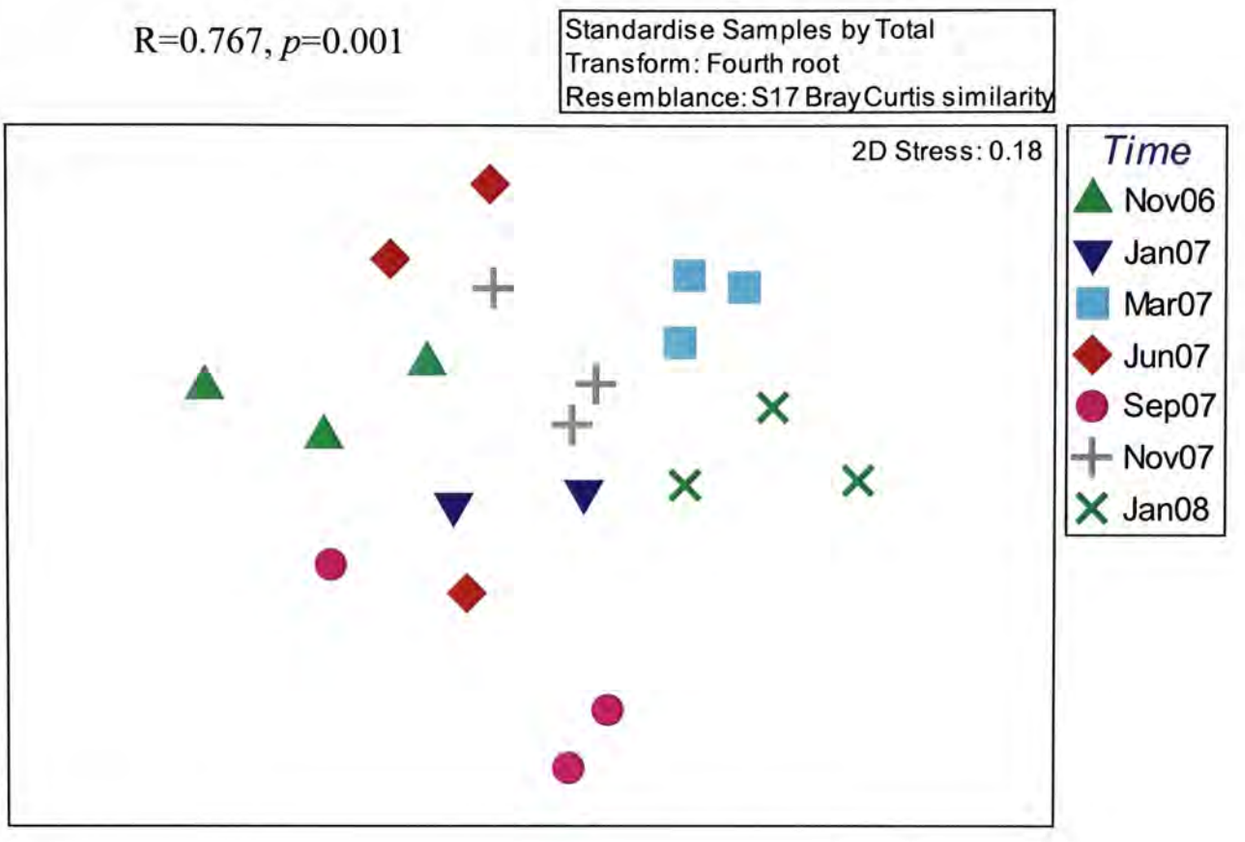


Fig. 2.5 MDS ordination plot showing the structure of zooplankton assemblage among sampling months in vegetated habitat in LLT (stress = 0.18). Each point represents data for each zooplankton tow in vegetated habitat over the sampling period from November 06 to January 08. ANOSIM results (with Global-R = 0.767) indicate significant separation in the structure of zooplankton assemblages among groups.

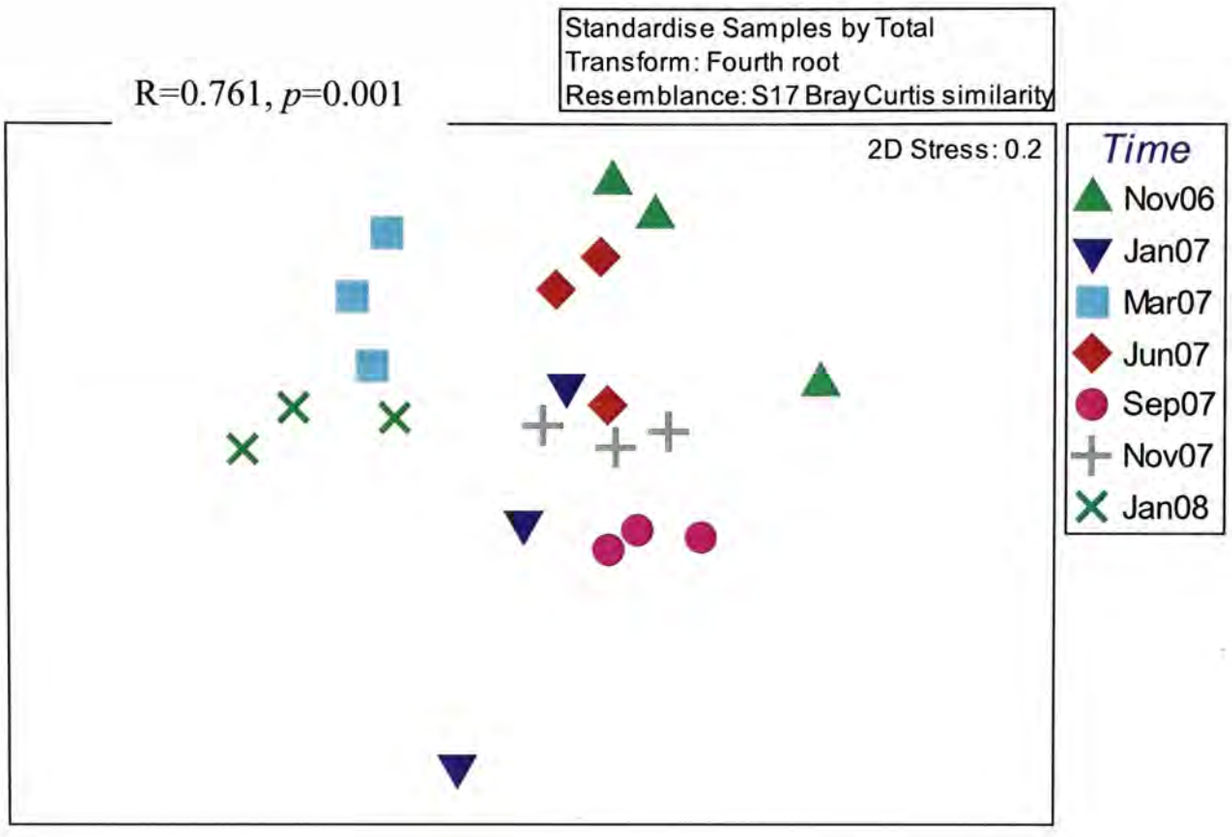


Fig. 2.6 MDS ordination plot showing the structure of zooplankton assemblage among sampling months in unvegetated habitat in LLT (stress = 0.2). Each point represents data for each zooplankton tow in unvegetated habitat over the sampling period from November 06 to January 08. ANOSIM results (with Global-R = 0.761) indicate significant separation in the structure of zooplankton assemblages among groups.

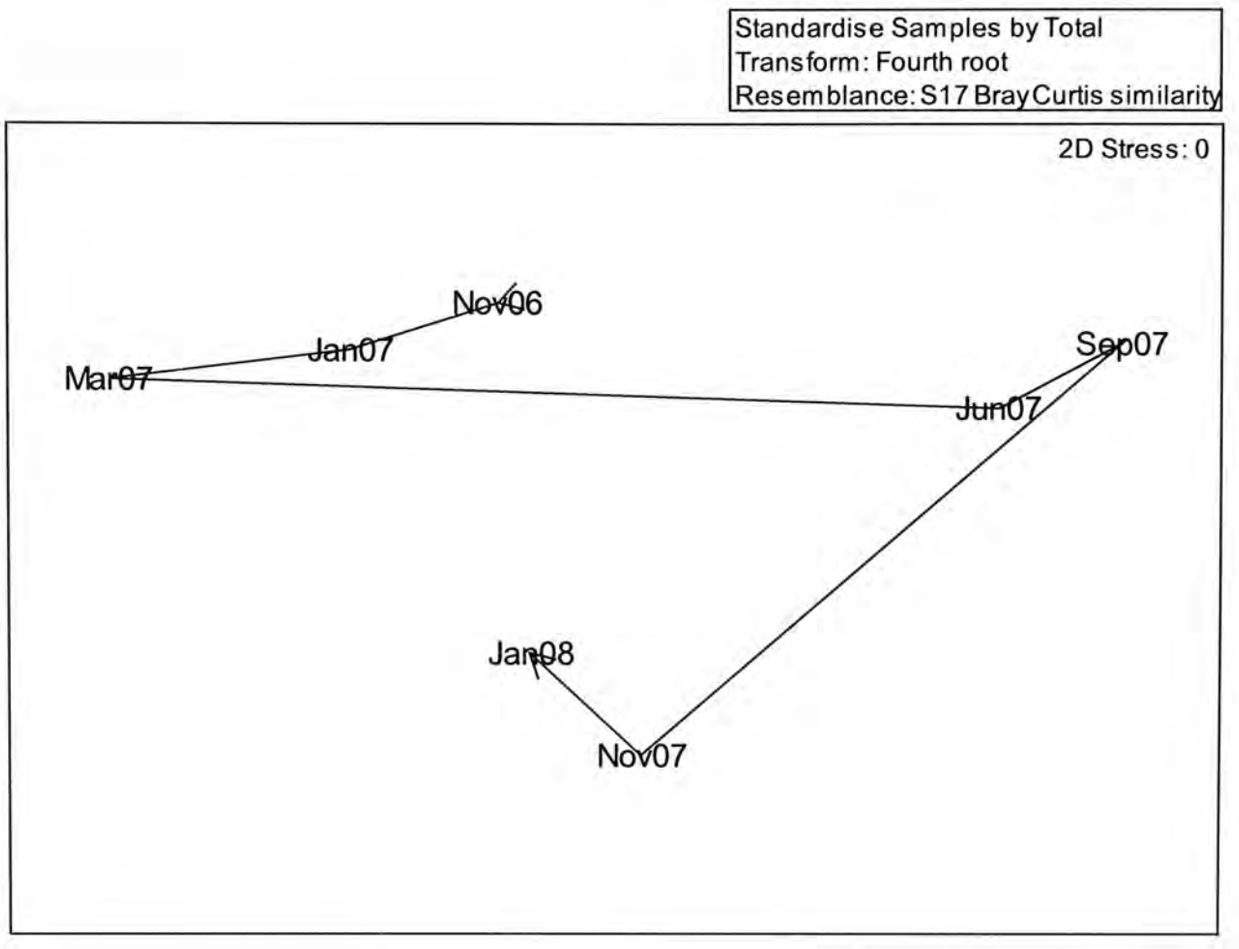


Fig. 2.7 MDS ordination plot showing the temporal shift in the structure of zooplankton assemblages in vegetated habitat in LFN (stress = 0). Each point represents mean of three zooplankton tows in vegetated habitat in each sampling month from November 06 to January 08.

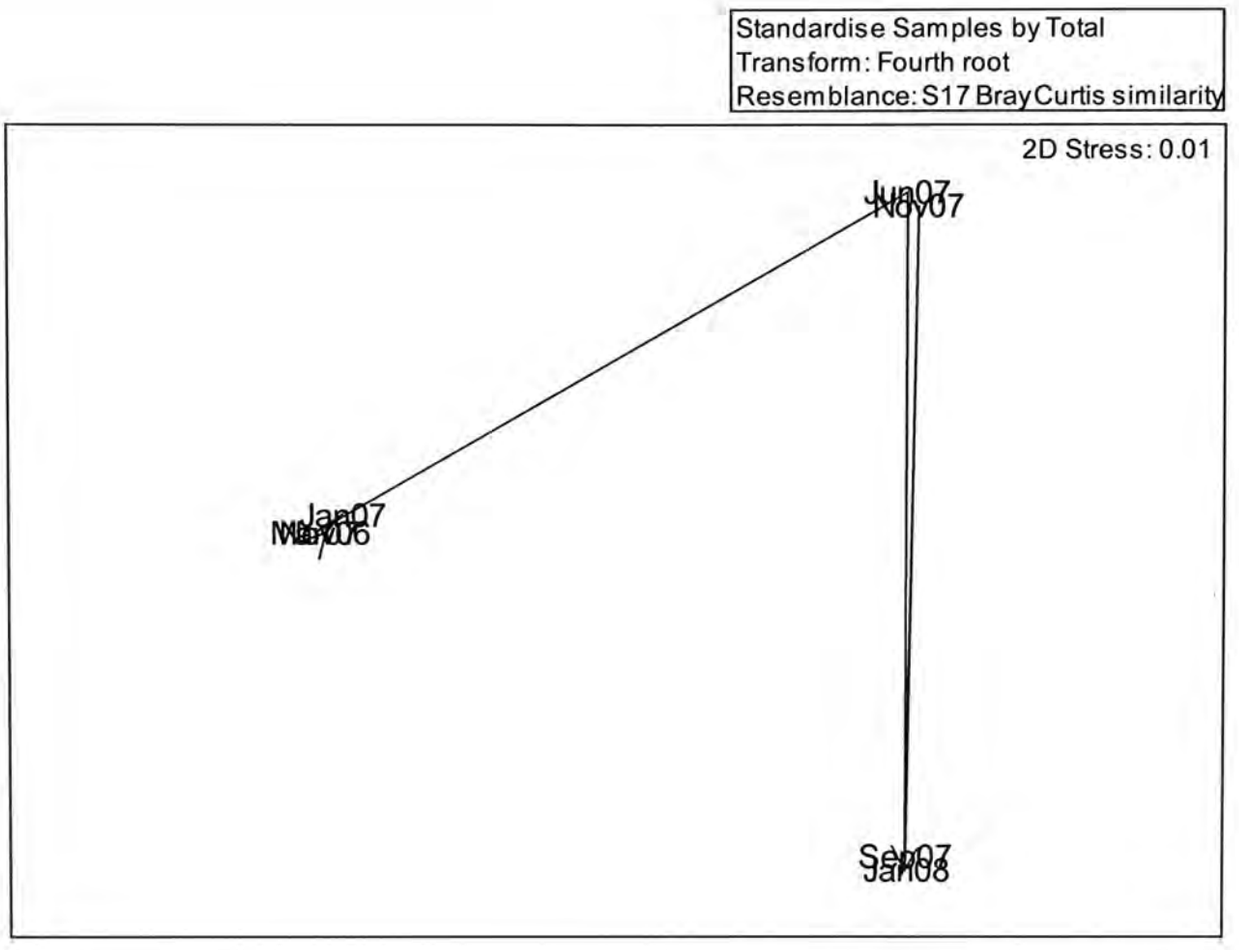


Fig. 2.8 MDS ordination plot showing the temporal shift in the structure of zooplankton assemblages in unvegetated habitat in LFN (stress = 0.01). Each point represents mean of three zooplankton tows in each sampling period from November 06 to January 08 in unvegetated habitat.

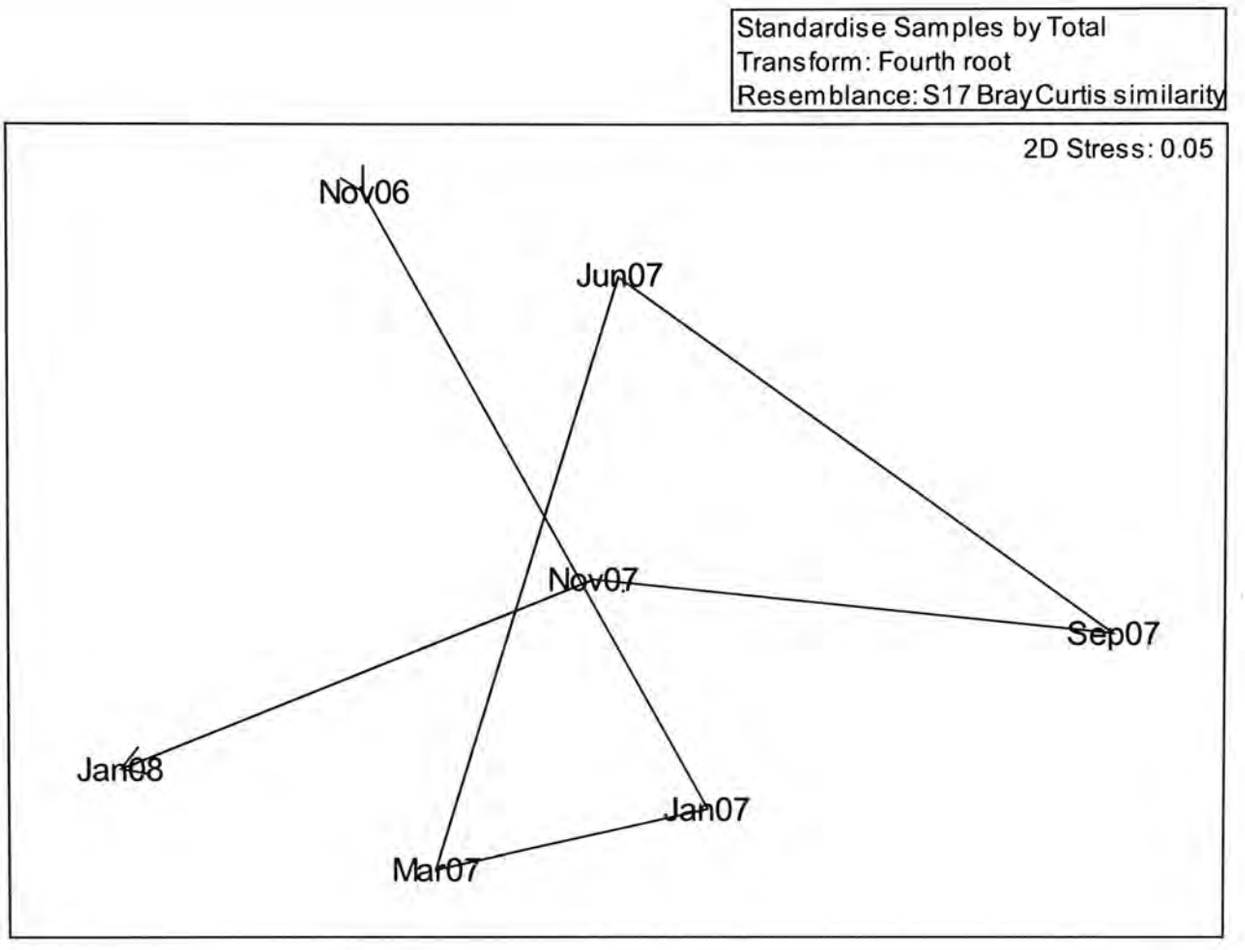


Fig. 2.9 MDS ordination plot showing the temporal shift in the structure of zooplankton assemblages in vegetated habitat in LLT (stress = 0.05). Each point represents mean of three zooplankton tows [except in Jan07, only two tows were averaged] in vegetated habitat in each sampling period from November 06 to January 08.

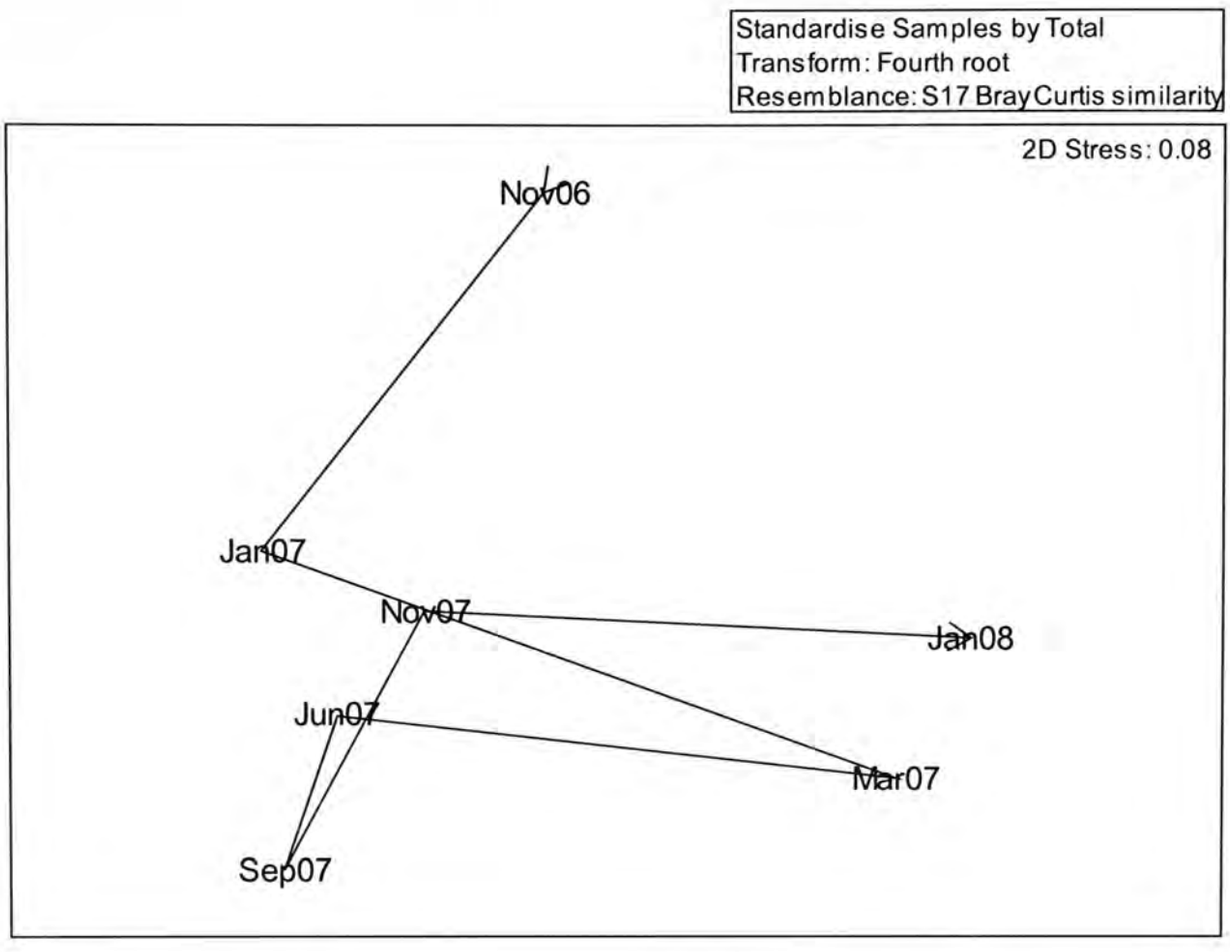


Fig. 2.10 MDS ordination plot showing the temporal shift in the structure of zooplankton assemblages in unvegetated habitat in LLT (stress = 0.08). Each point represents mean of three zooplankton tows in unvegetated habitat in each sampling period from November 06 to January 08.

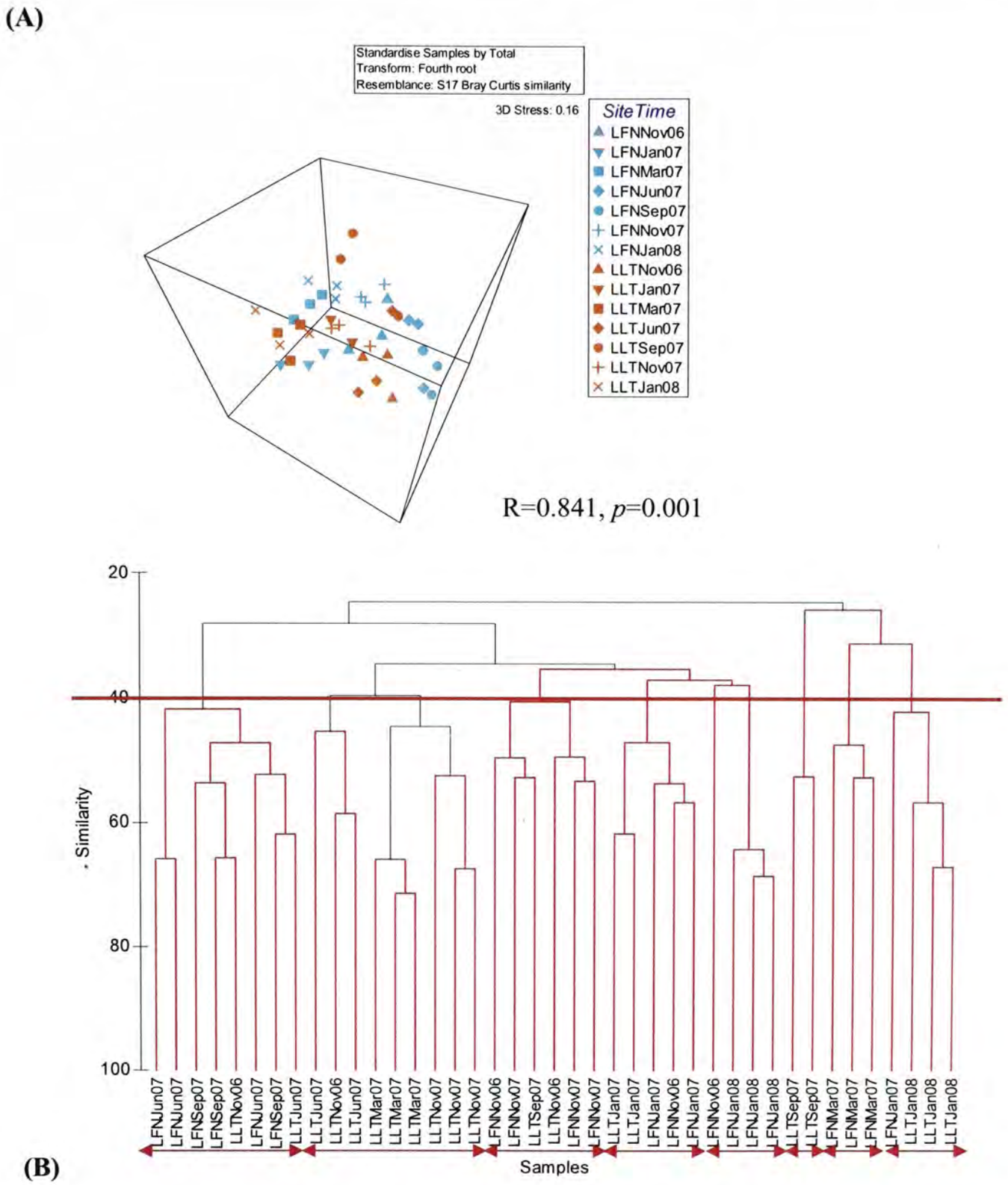


Fig. 2.11 (**A**).MDS ordination plot (stress = 0.16) and (**B**).Dendrogram based on Bray-Curtis similarity among fourth root transformed group averaged data with 1000 times of permutation showing respectively the structure and similarity of zooplankton assemblage among sampling months in vegetated habitat in LFN and LLT. Each point represents data for each zooplankton tow in each sampling month at different site. ANOSIM results (with Global-R = 0.841) indicate significant separation in the structure of zooplankton assemblages among groups. Solid lines in dendrogram display groupings which are statistically significant (Simprof test, $p<0.05$). For grouping patterns, refer to the dendrograms and the text.

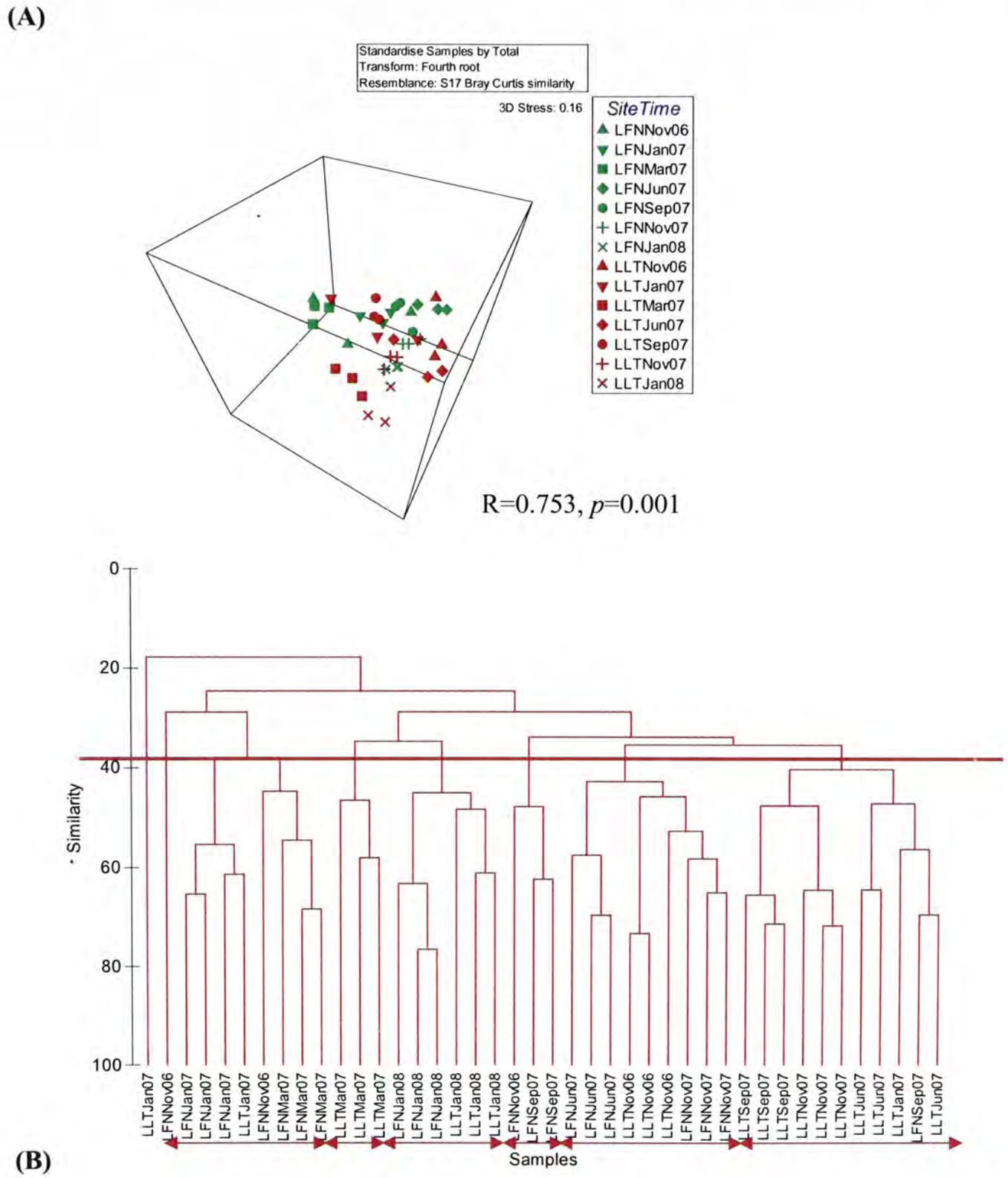


Fig. 2.12 (**A**).MDS ordination plot (stress = 0.16) and (**B**).Dendrogram based on Bray-Curtis similarity among fourth root transformed group averaged data with 1000 times of permutation showing respectively the structure and similarity of zooplankton assemblage among sampling months in unvegetated habitat in LFN and LLT. Each point represents data for each zooplankton tow in each sampling month at different site. ANOSIM results (with Global-R = 0.753) indicate significant separation in the structure of zooplankton assemblages among groups. Solid lines in dendrogram display groupings which are statistically significant (Simprof test, $p<0.05$). For grouping patterns, refer to the dendrogram and the text.

Vegetated: Chi-square= 9.229, df= 6, p=0.161

Unvegetated: Chi-square= 16.288, df= 6, p=0.012

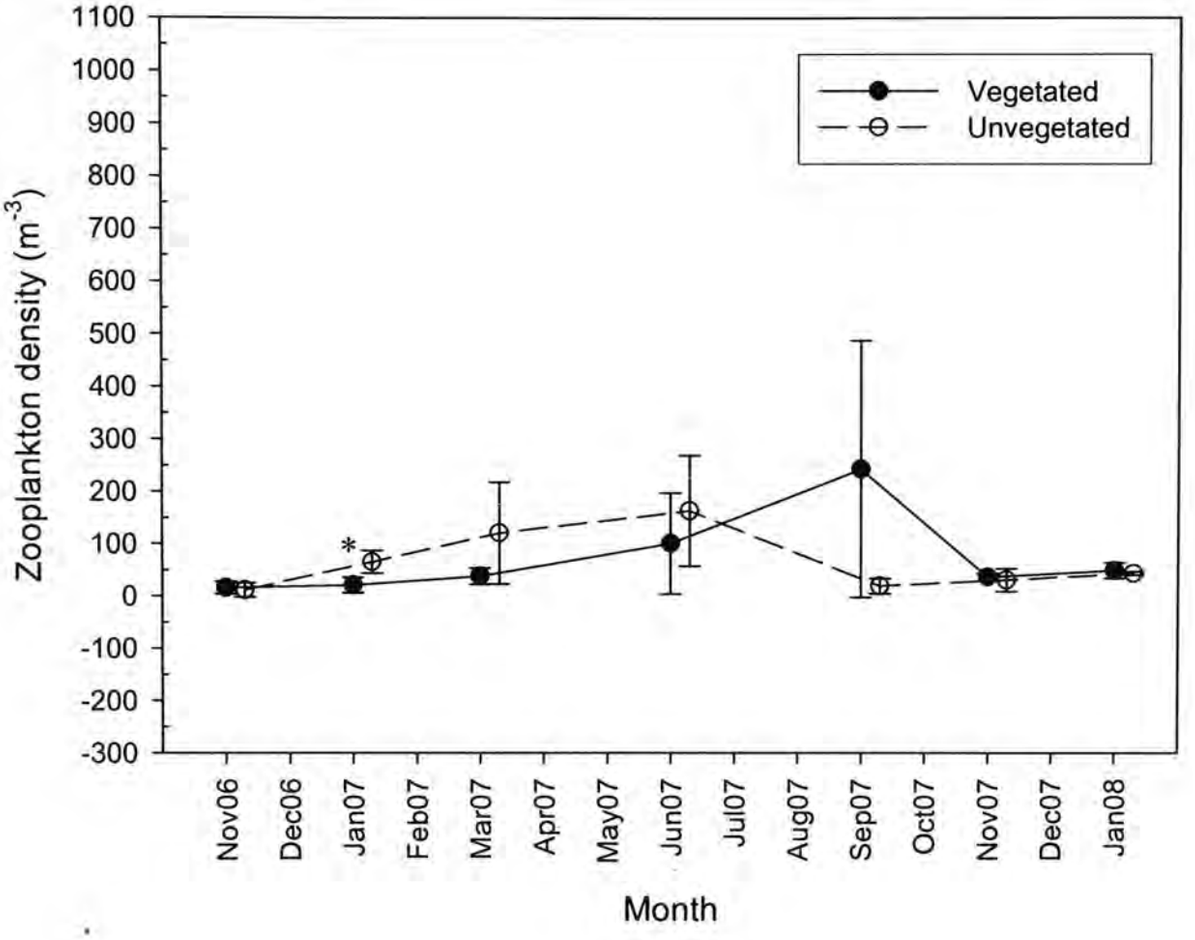


Fig. 2.13 Temporal change in ge Kruskal Wallis test showed significant differences in mean zooplankton density between months only in unvegetated habitat. Student t-test result (df = 4) displayed significant difference in mean zooplankton density between vegetated and unvegetated habitats only in Jan 07 (p = 0.045) (as marked by *).

Vegetated: Chi-square = 12.173, df =6 , p =0.058

Unvegetated: Chi-square = 13.294, df = 6, p =0.039

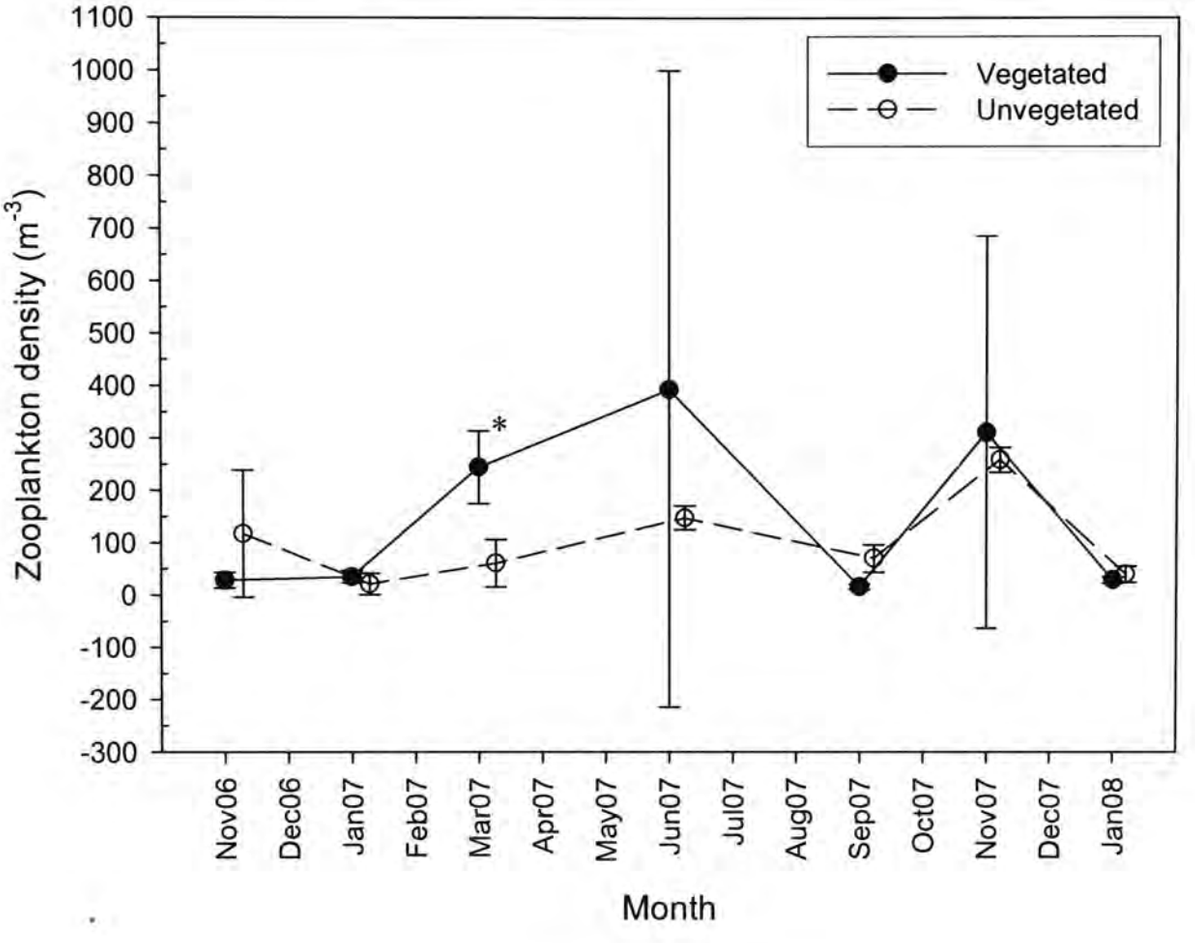


Fig. 2.14 Temporal change in mean (± S.D.) zooplankton density in vegetated and unvegetated habitats in LLT. Kruskal Wallis test showed significant differences in mean zooplankton density between months only in unvegetated habitat. Student t-test result (df = 4) displayed significant difference in mean zooplankton density between vegetated and unvegetated habitats only in Mar 07 (p = 0.019) (as marked by *).

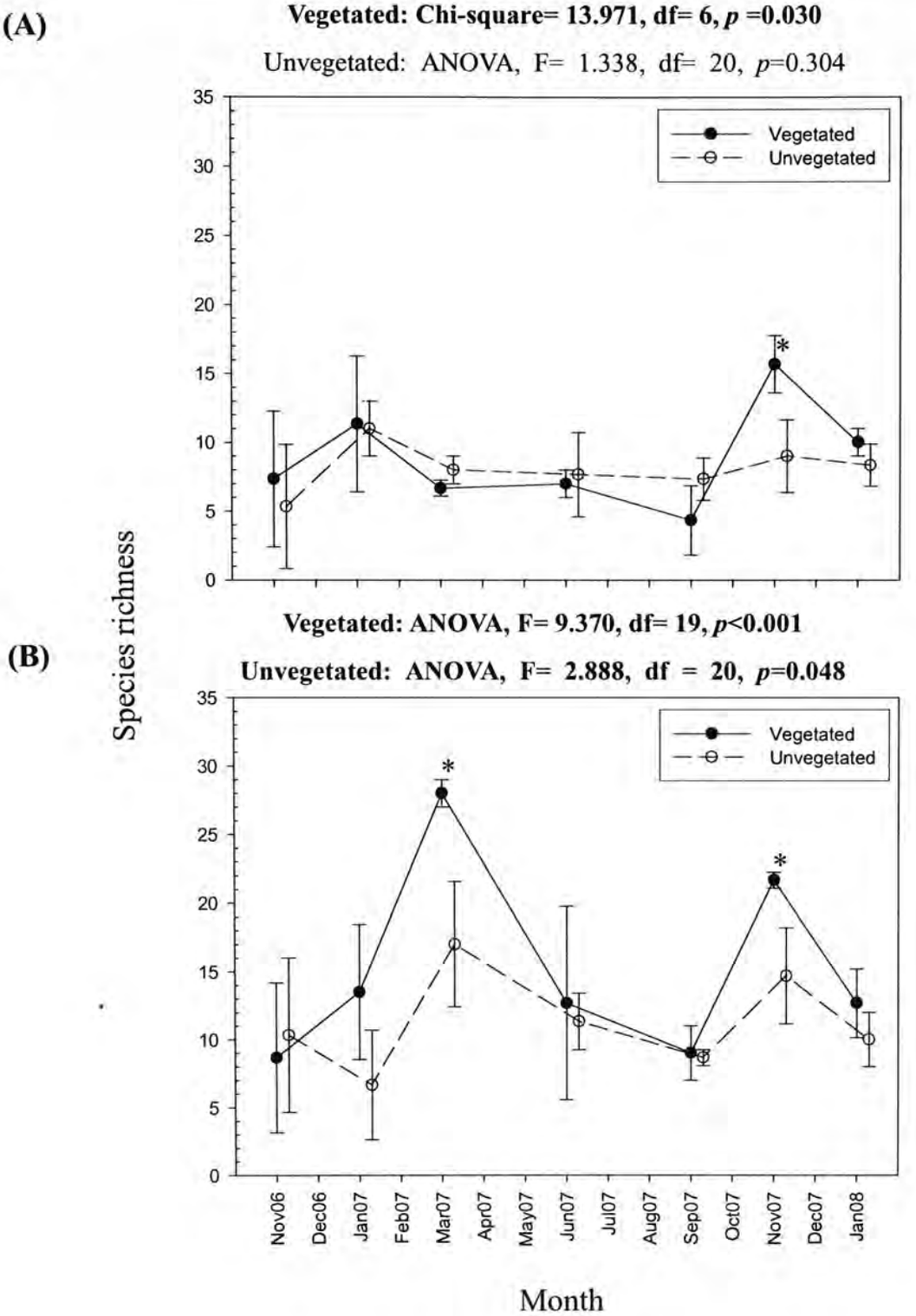


Fig. 2.15 Temporal change in mean (± S.D.) species richness in vegetated and unvegetated habitats in **(A)** LFN and **(B)** LLT. One-way ANOVA and Kruskal Wallis test results showed significant differences in species richness between months in all habitats except the unvegetated habitat in LFN. Student *t*-test results (df = 4) detected significant differences in mean species richness between vegetated and unvegetated habitats in Nov07 (p = 0.027) at LFN as well as in Mar07 (p = 0.015) and Nov07 (p = 0.027) at LLT (as marked by *).

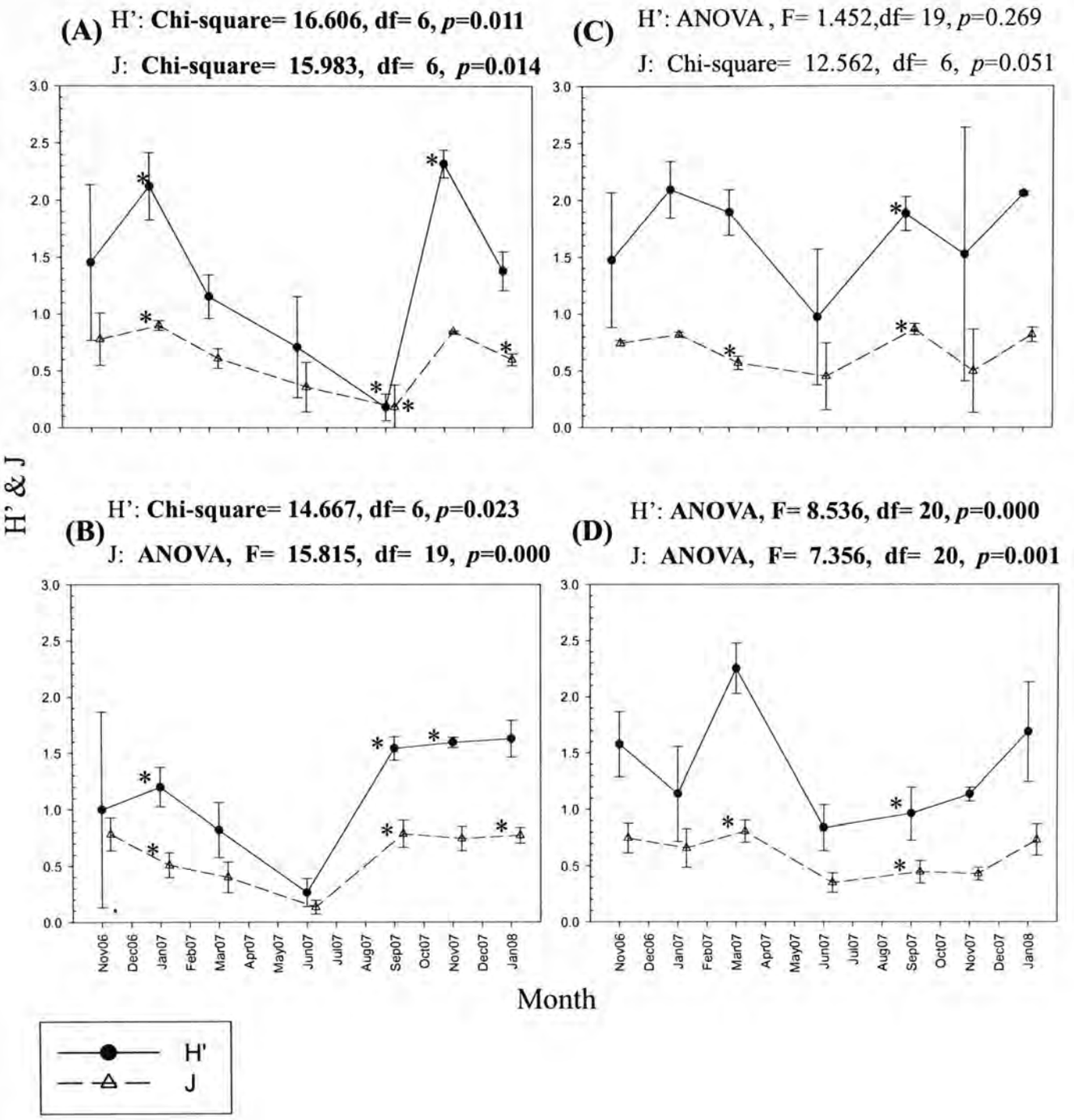


Fig. 2.16 Temporal change in mean (± S.D.) Shannon Diversity (H') and Evenness (J) Indices in (**A**) vegetated and (**B**) unvegetated habitats in LFN and in (**C**).vegetated and (**D**).unvegetated habitats in LLT. One-way ANOVA and Kruskal Wallis test results showed significant differences in H' and J between months in all habitats except the vegetated habitat in LLT. Student *t*-test results (df = 4) detected significant differences in mean H' between vegetated and unvegetated habitats in Jan07 ($p = 0.010$), Sep07 ($p < 0.001$) and Nov07 ($p = 0.001$) at LFN as well as in Sep07 ($p = 0.005$) at LLT; in mean J between habitat types in Jan07 ($p = 0.005$), Sep07 ($p = 0.010$) and Jan08 ($p = 0.025$) at LFN as well as in Mar07 ($p = 0.025$) and Sep07 ($p = 0.003$) at LLT (as marked by *).

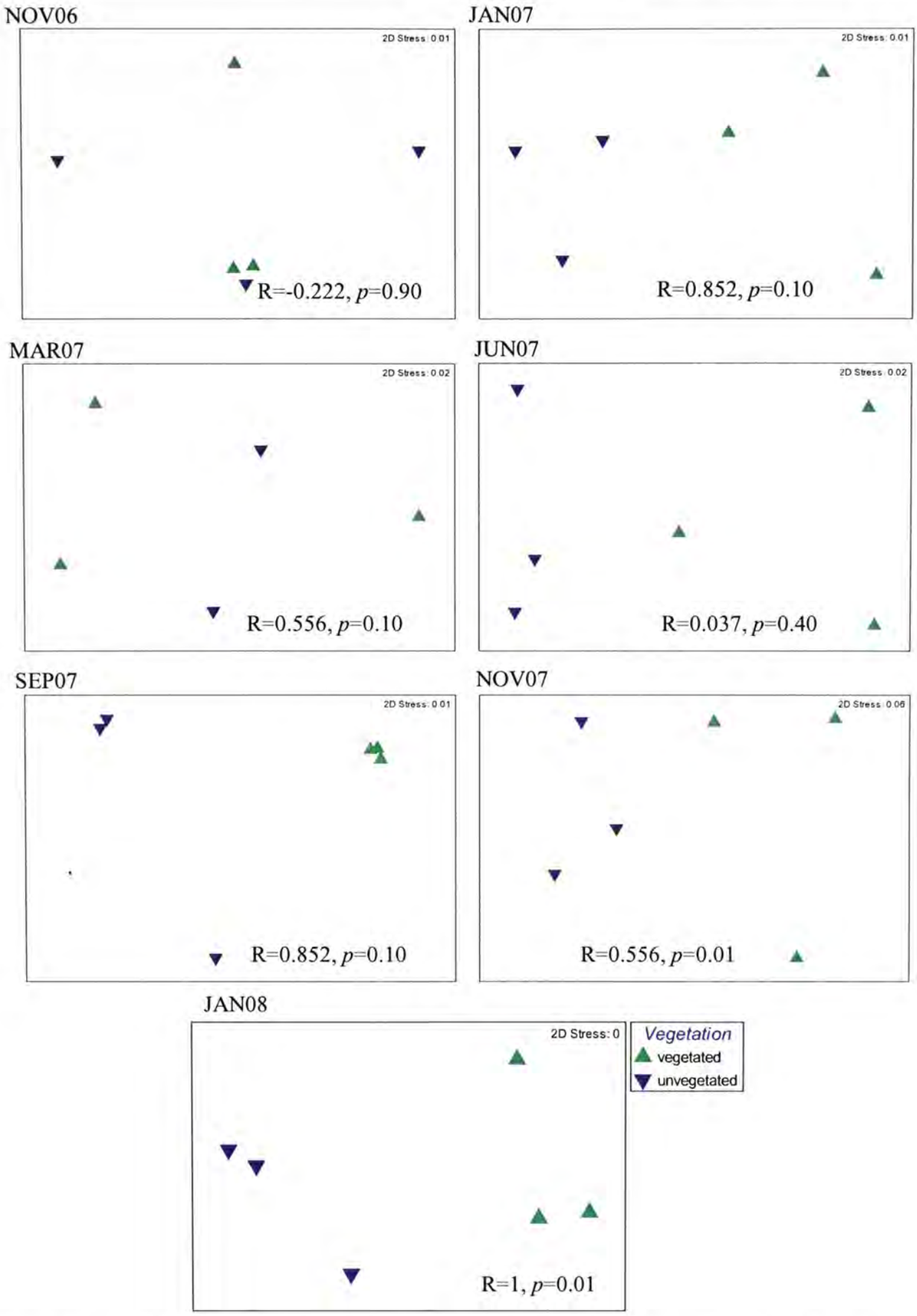


Fig. 2.17 MDS ordination plot based on Bray-Curtis similarities showing the structure of zooplankton assemblage between vegetated and unvegetated habitats in each sampling month from November 06 to January 08 in LFN. Each point represents data for each zooplankton tow. ANOSIM results in Jan07, Mar07, Sep07, Nov07 and Jan08 indicate more distinct separation in the structure of zooplankton assemblages between groups in vegetated and unvegetated habitats, though without statistical significance.

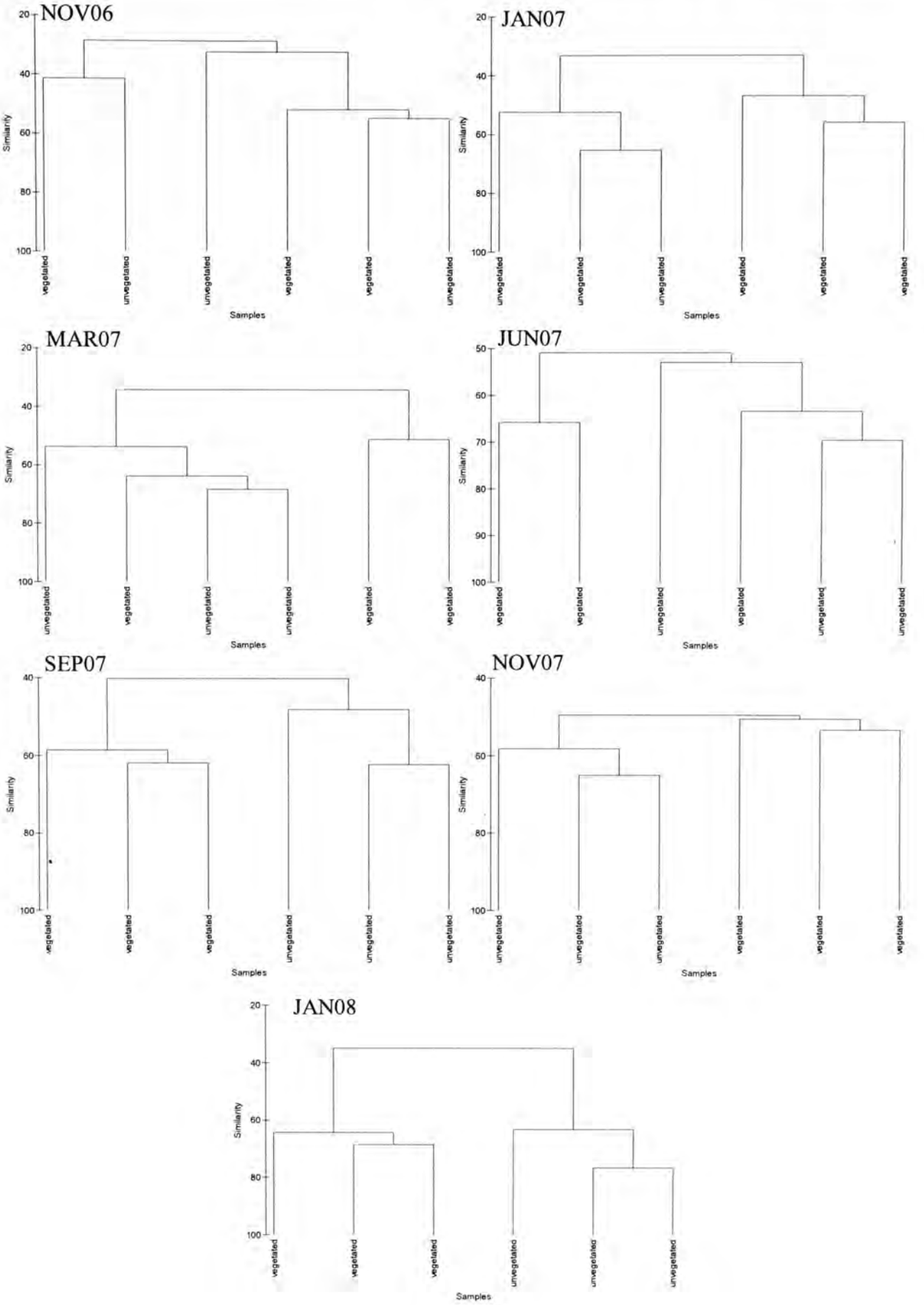


Fig. 2.18 Dendrogram based on Bray-Curtis similarity among fourth root transformed group average data showing the similarity of zooplankton assemblage between vegetated and unvegetated habitats in each sampling month from November 06 to January 08 in LFN.

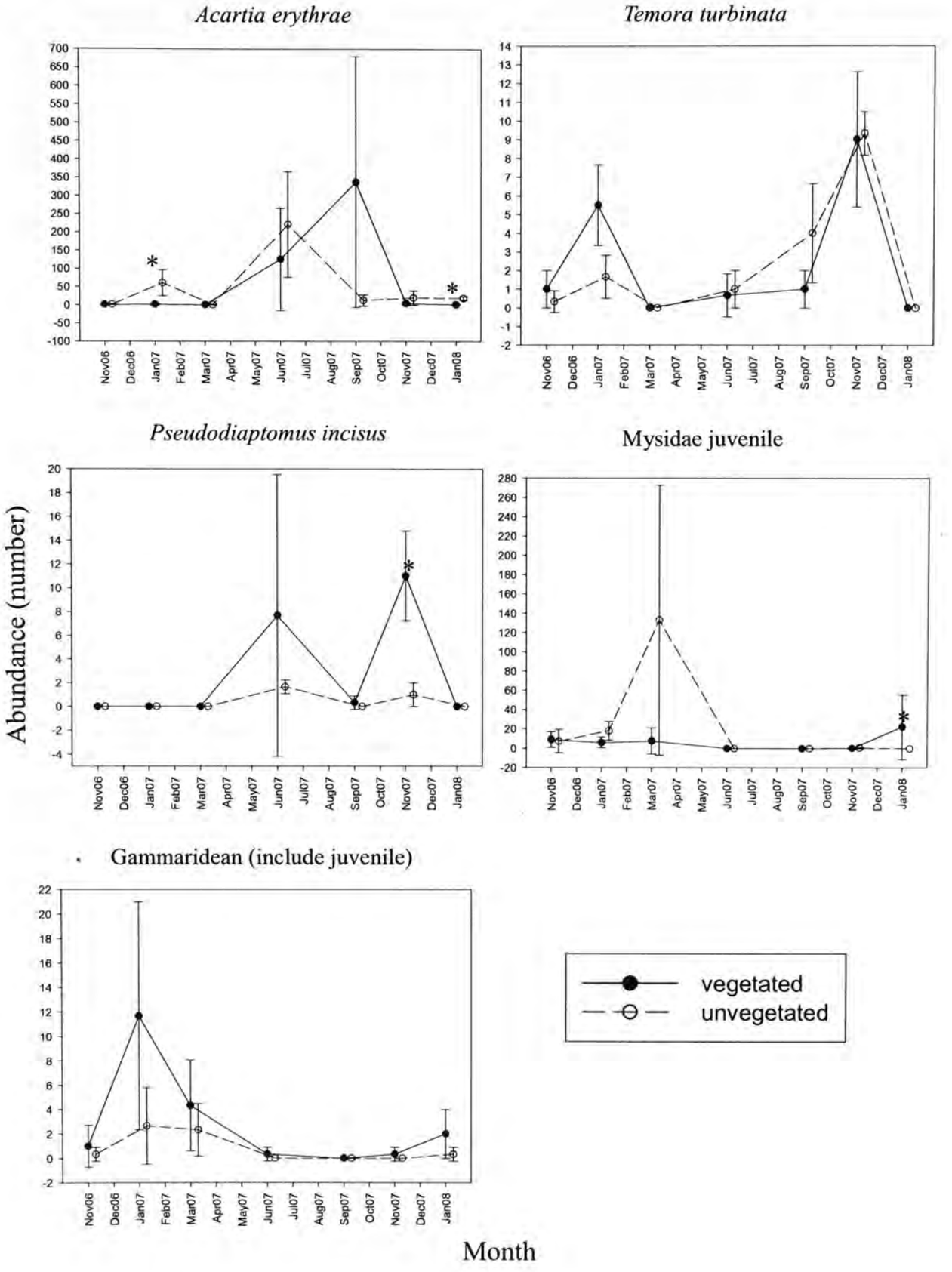


Fig. 2.19 Temporal change in abundance of differentiating species between vegetated and unvegetated habitats in LFN. Student *t*-test and Mann-Whitney test results ($p<0.05$, df = 4) showed significant differences in mean abundance of some taxa between vegetated and unvegetated habitats in some sampling months (as marked by *).

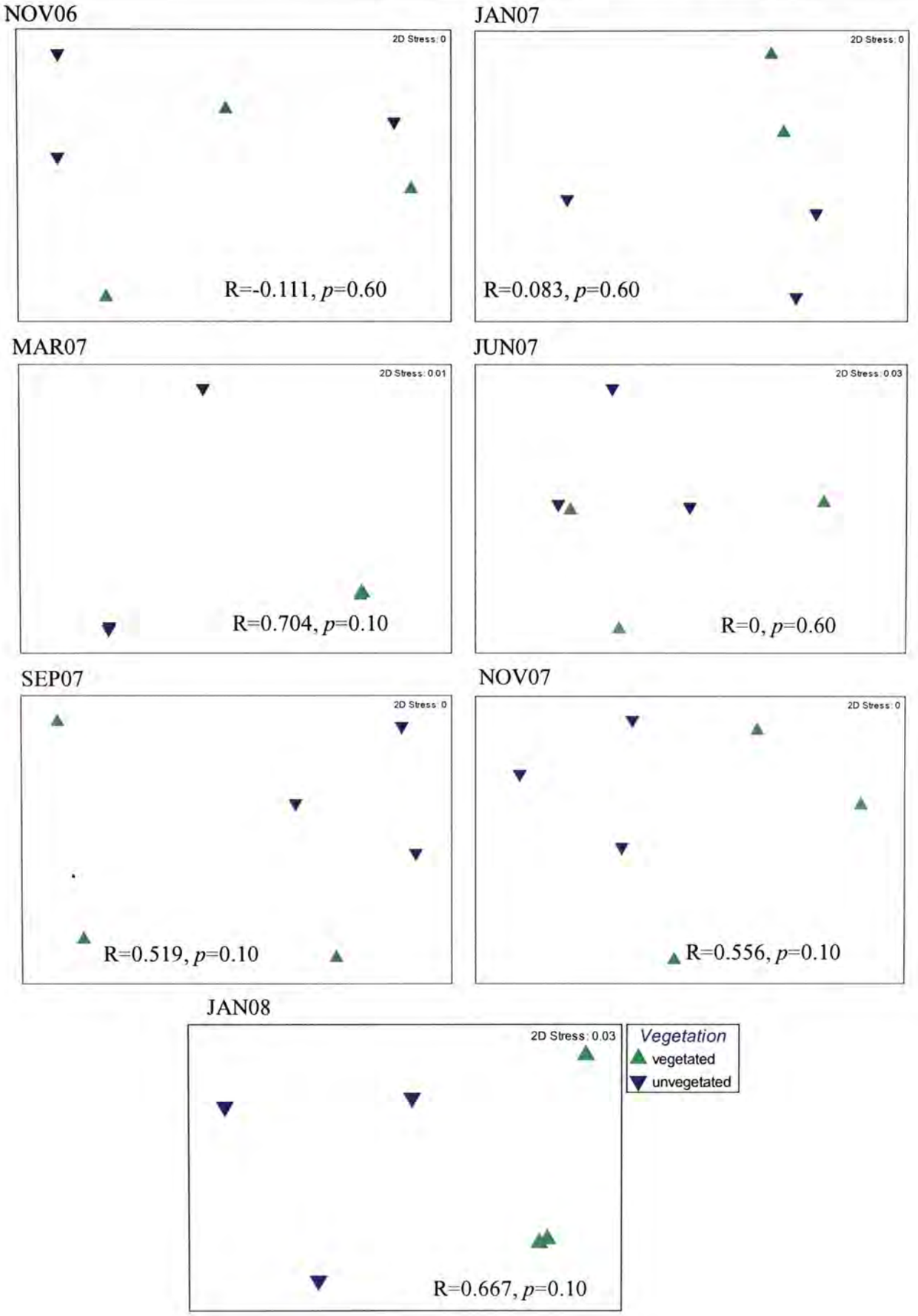


Fig. 2.20 MDS ordination plot based on Bray-Curtis similarities showing the structure of zooplankton assemblage between vegetated and unvegetated habitats in each sampling month from November 06 to January 08 in LLT. Each point represents data for each zooplankton tow. ANOSIM results in Mar07, Sep07, Nov07 and Jan08 indicate more distinct separation in the structure of zooplankton assemblages between groups in vegetated and unvegetated habitats, though without statistical significance.

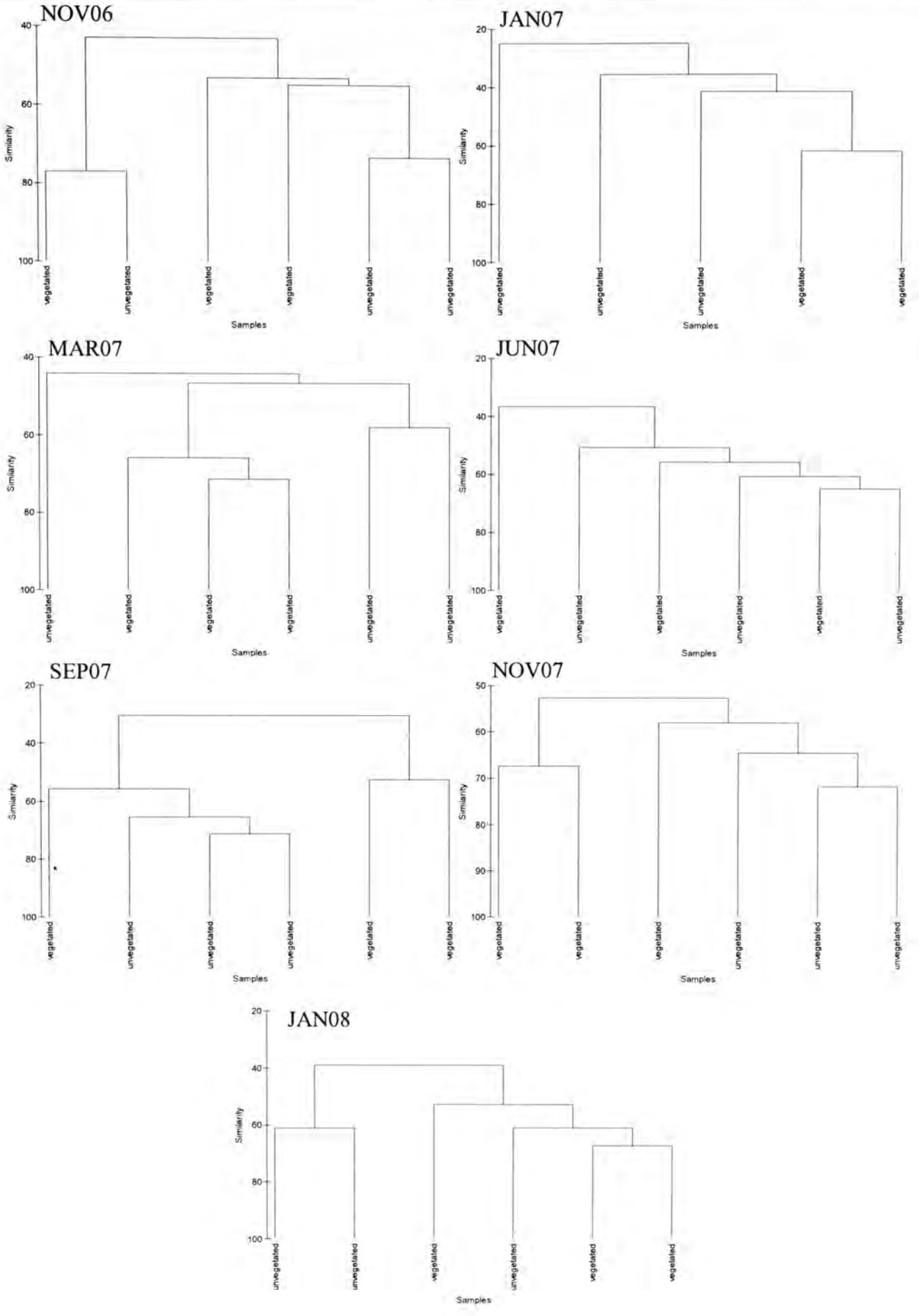


Fig. 2.21 Dendrogram based on Bray-Curtis similarity among Fourth root transformed group averaged data showing the similarity of zooplankton assemblages between vegetated and unvegetated habitats in each sampling month from November 06 to January 08 in LLT.

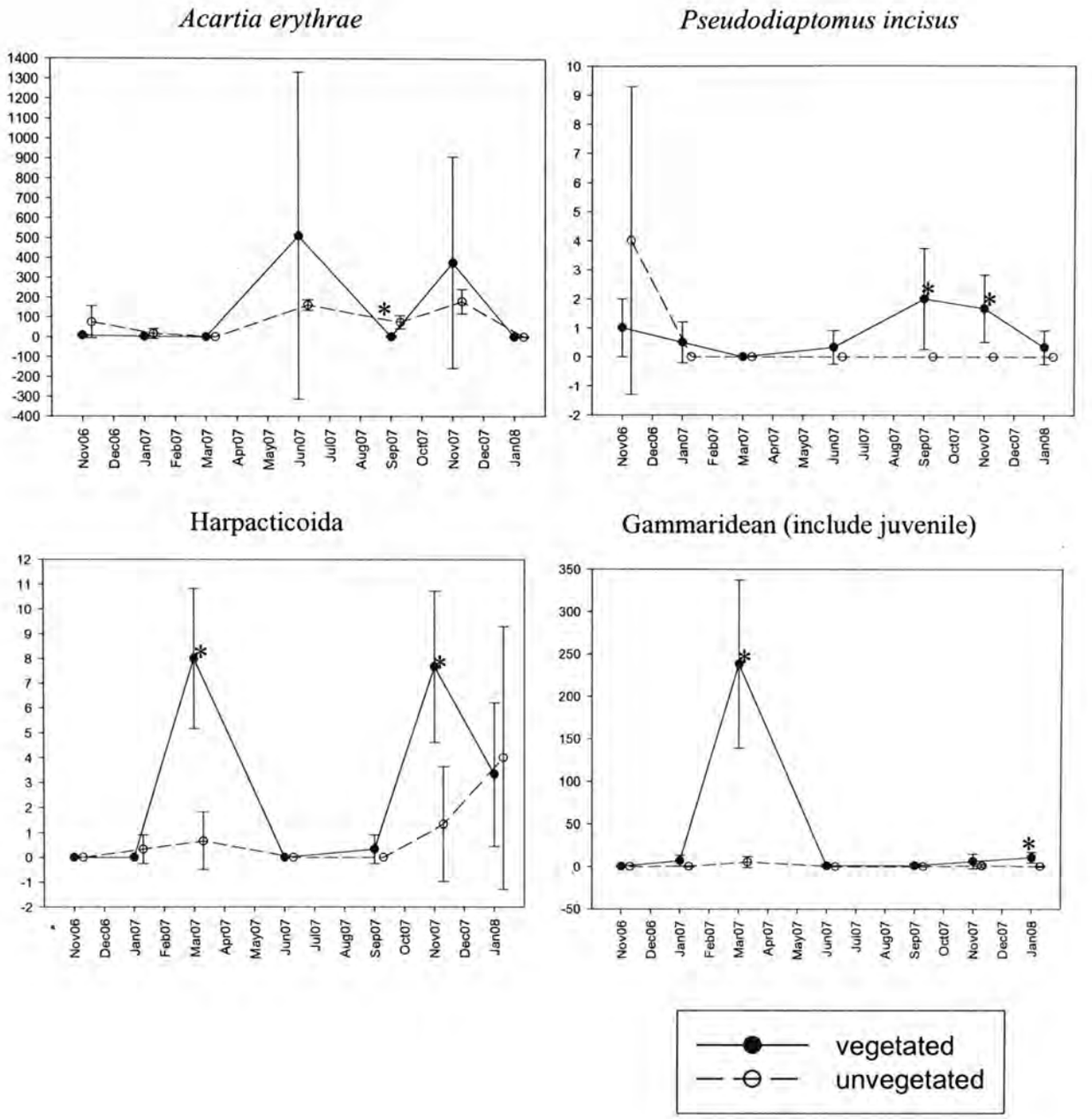


Fig. 2.22 Temporal change in the abundance of differentiating species between vegetated and unvegetated habitats in LLT. Student *t*-test and Mann-Whitney test results ($p<0.05$, df = 4) showed significant differences in mean abundance of some taxa between vegetated and unvegetated habitats in some sampling months (as marked by *).

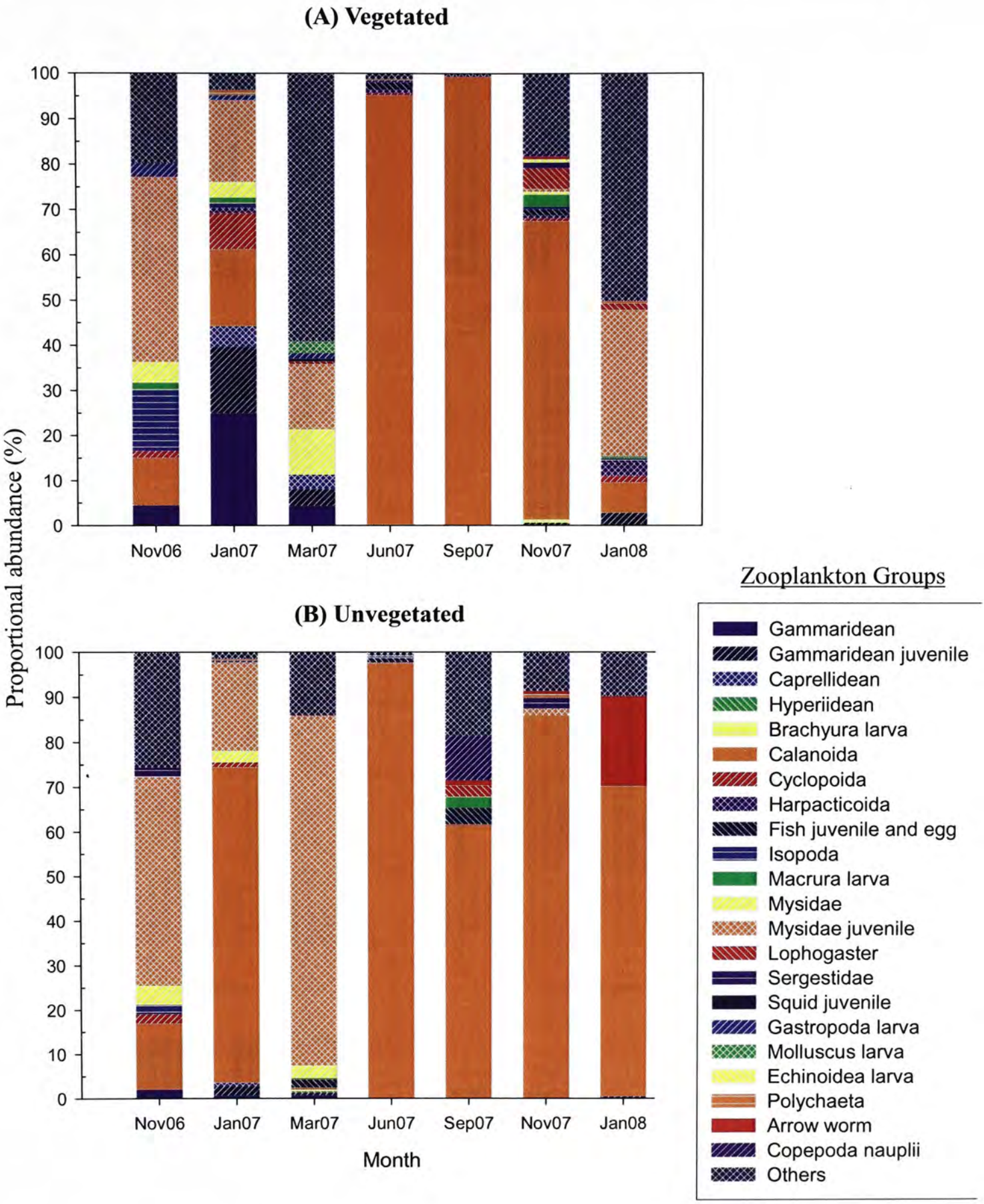


Fig. 2.23 Proportional abundance of zooplankton groups in (**A**).vegetated and (**B**).unvegetated habitats in each sampling month in LFN.

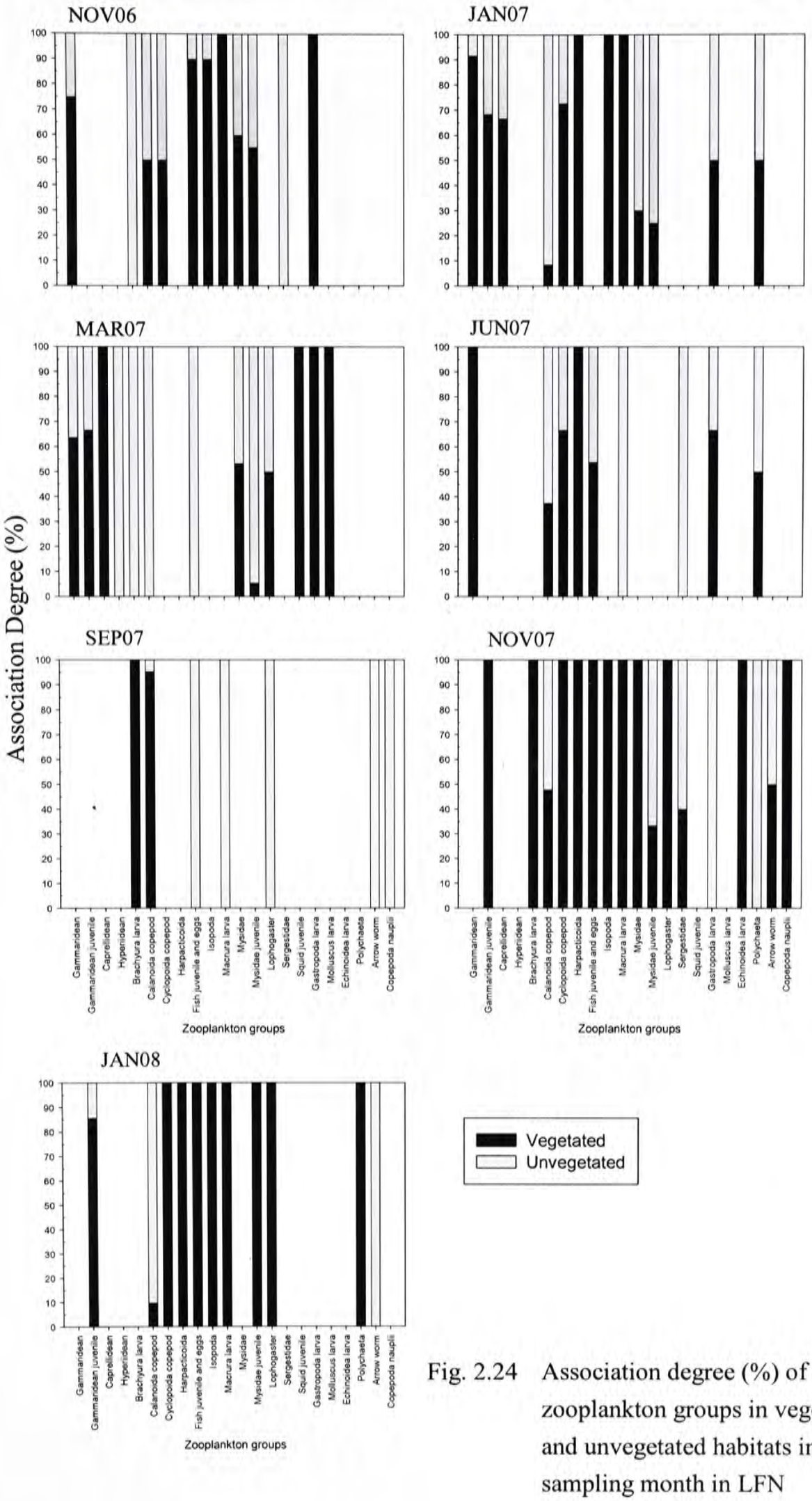


Fig. 2.24 Association degree (%) of common zooplankton groups in vegetated and unvegetated habitats in each sampling month in LFN

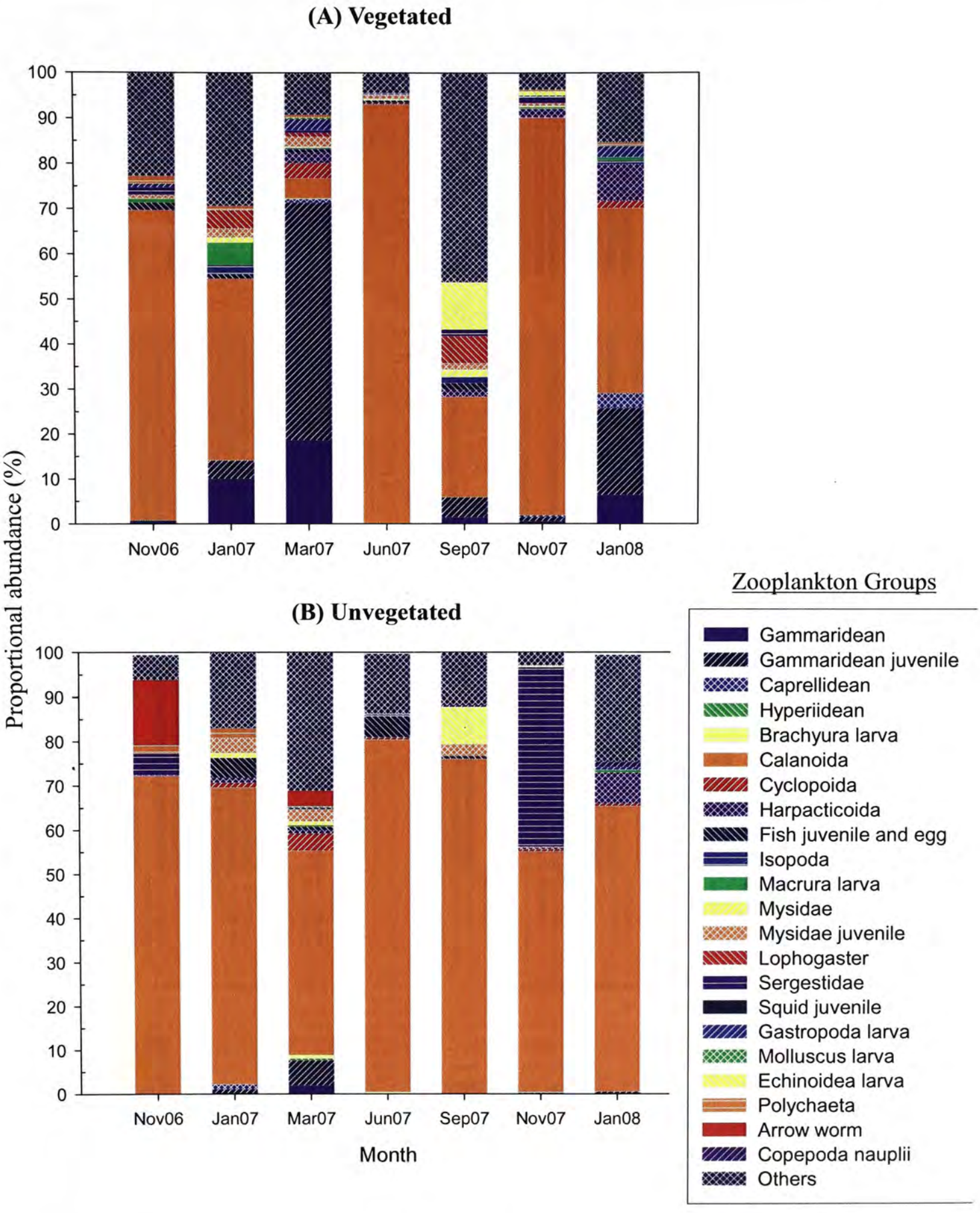


Fig. 2.25 Proportional abundance of zooplankton groups in (**A**).vegetated and (**B**).unvegetated habitats in each sampling month in LLT.

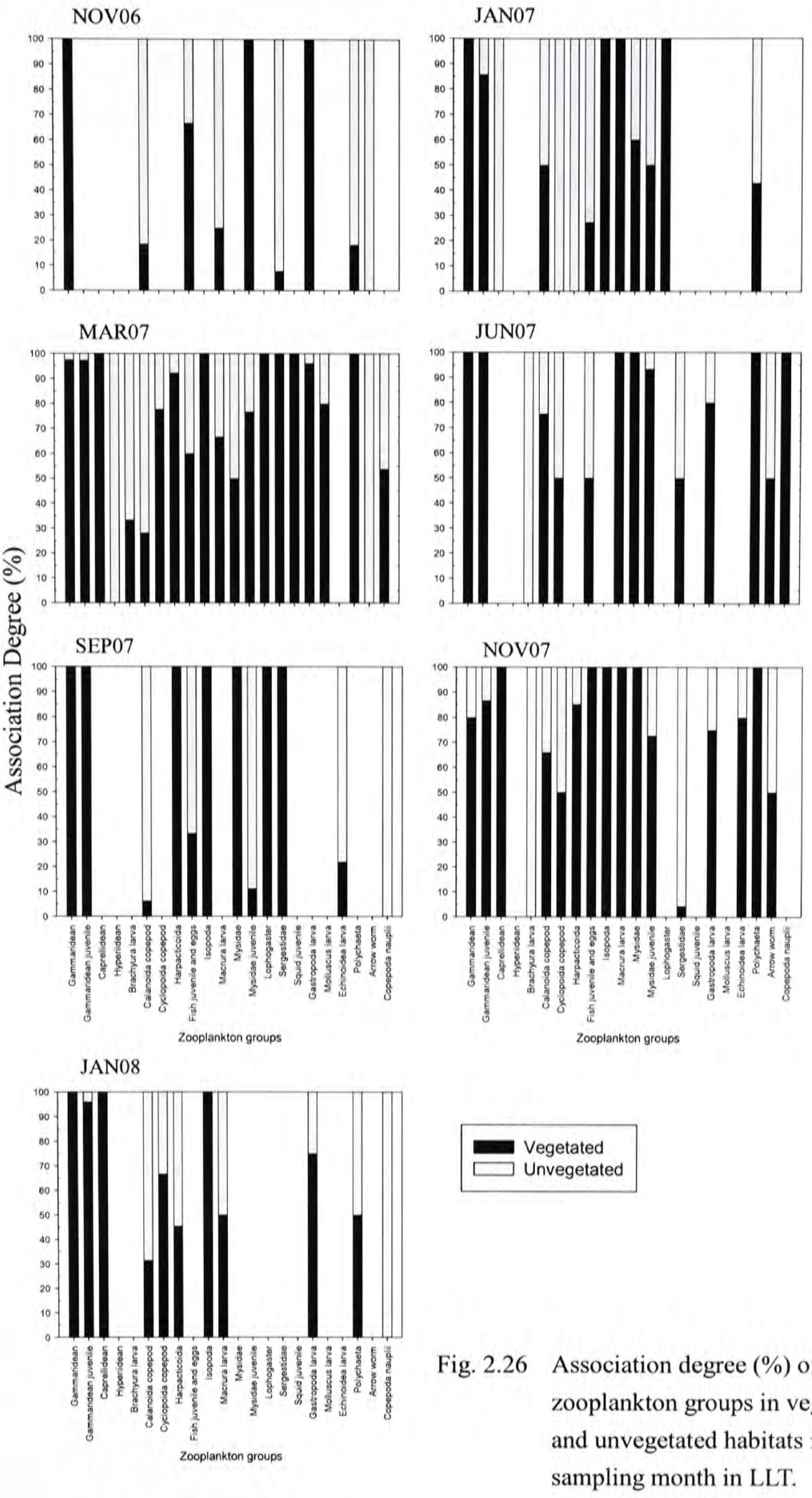
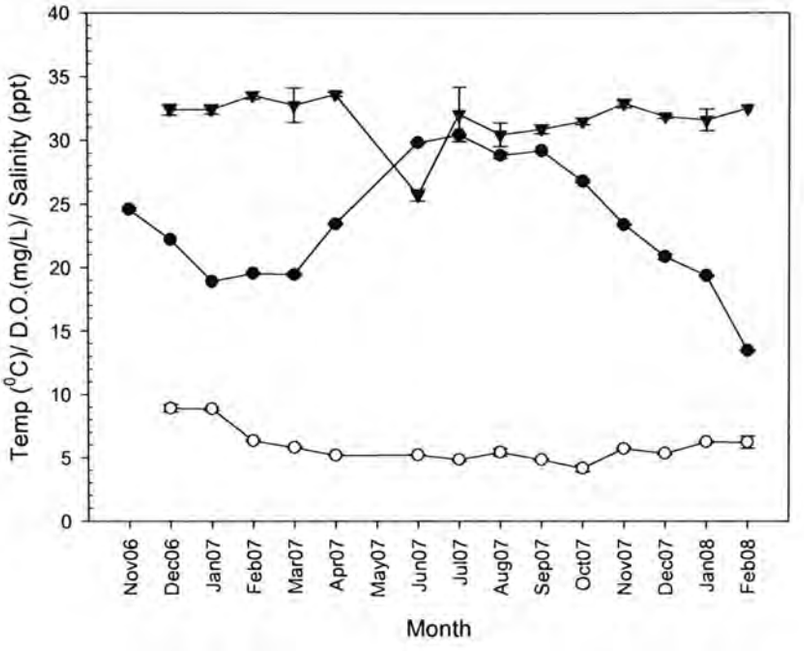


Fig. 2.26 Association degree (%) of common zooplankton groups in vegetated and unvegetated habitats in each sampling month in LLT.

(A) LFN



(B) LLT

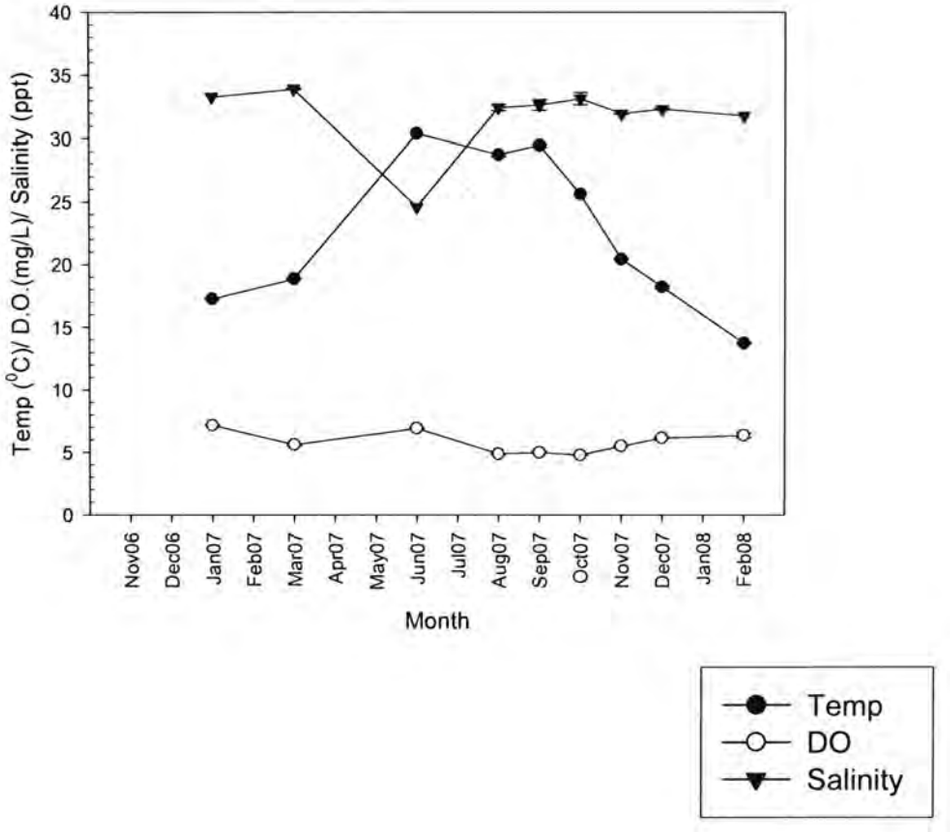


Fig. 2.27 Temporal change in mean (± S.D.) temperature, levels of dissolved oxygen and salinity (n = 3) over the sampling period from November 06 to February 08 in (**A**). LFN and (**B**). LLT.

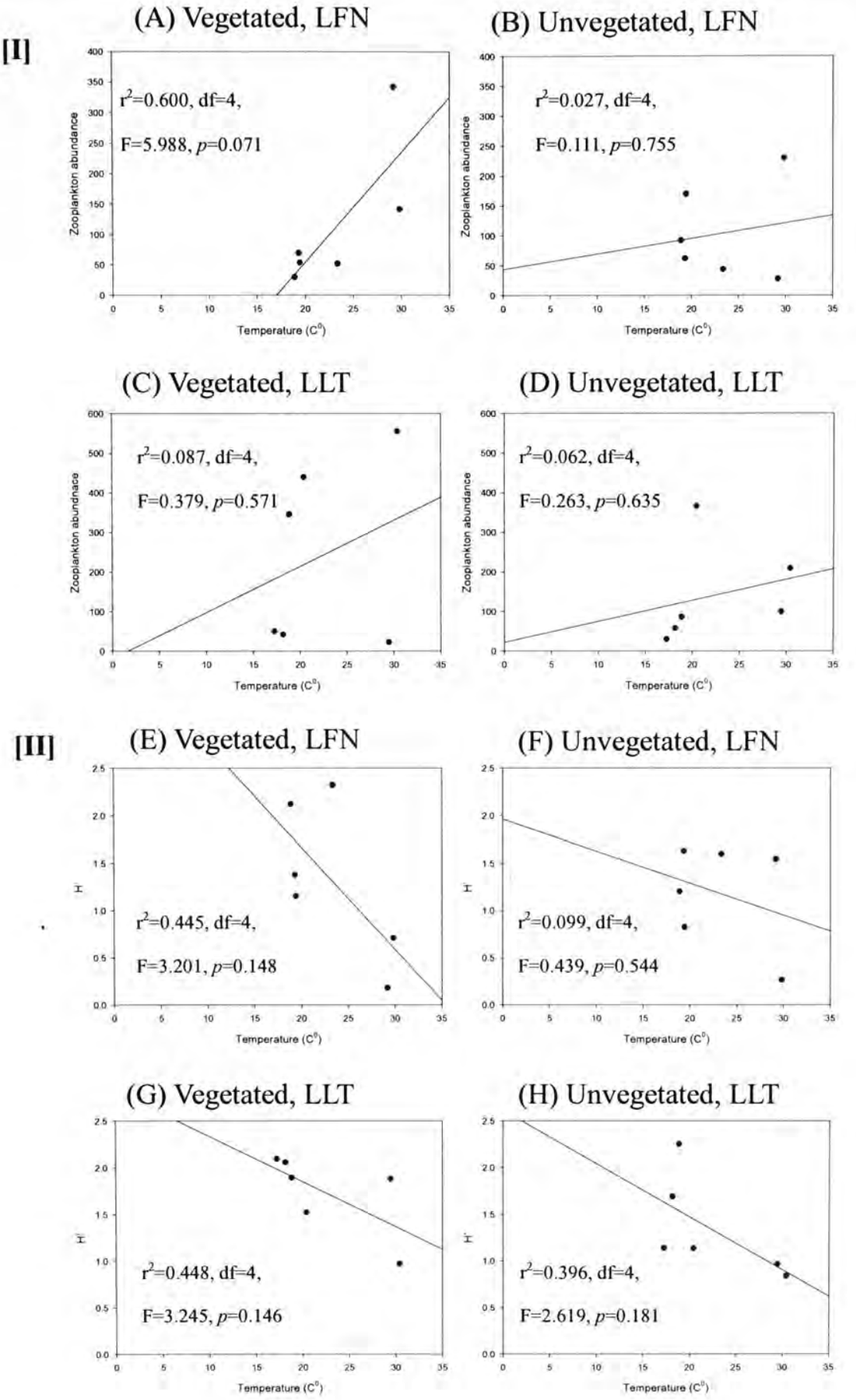


Fig. 2.28 Relationship between temperature and zooplankton [**I**]. abundance; [**II**]. Shannon diversity index (H'), in vegetated and unvegetated habitats in LFN and LLT. Regression analyses indicate all relationships to be not statistically significant. Regression equations not shown.

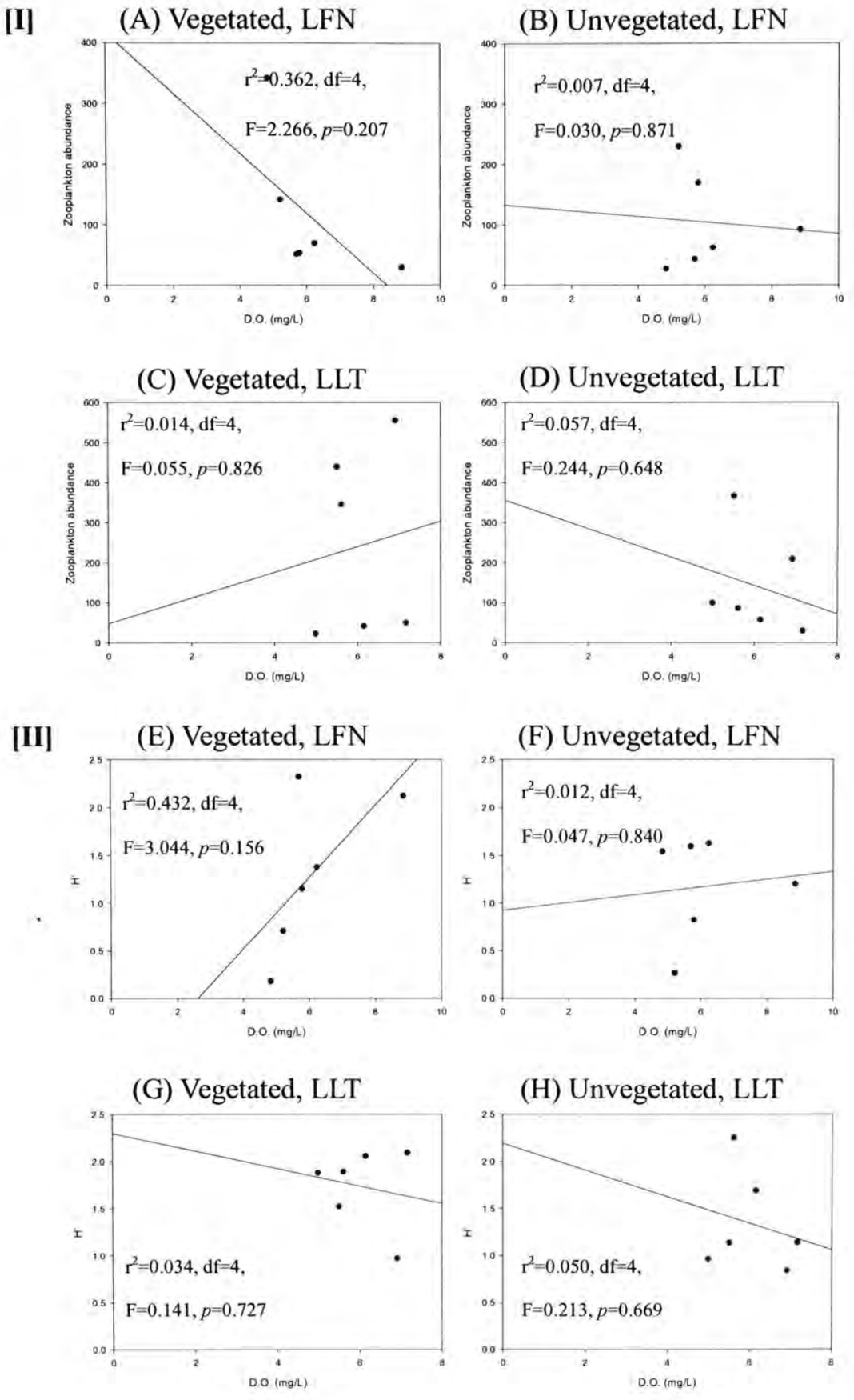


Fig. 2.29 Relationship between dissolved oxygen concentration and zooplankton [**I**]. abundance; [**II**]. Shannon diversity index (H'), in vegetated and unvegetated habitats in LFN and LLT. Regression analyses indicate all relationships to be not statistically significant. Regression equations not shown.

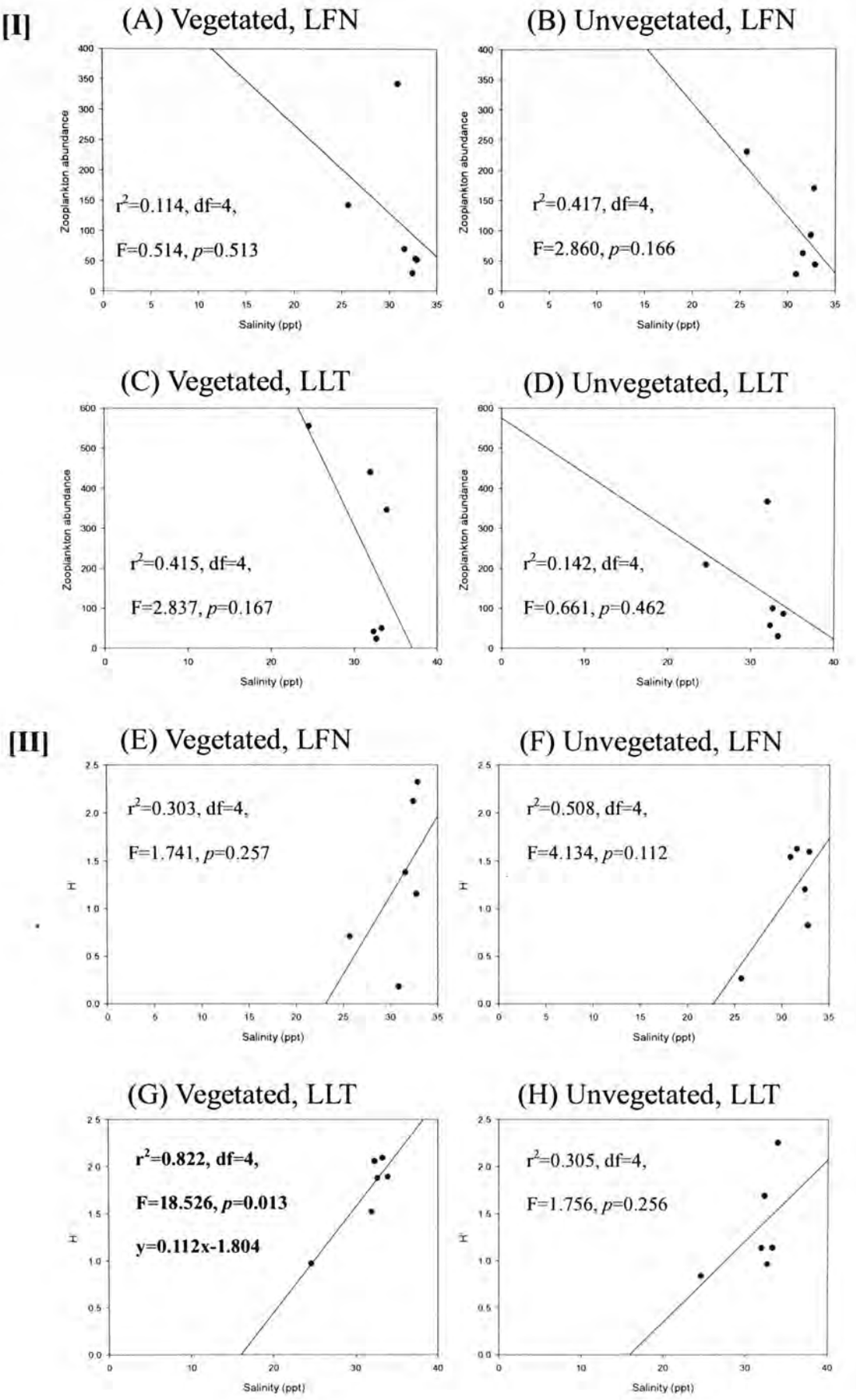


Fig. 2.30 Relationship between salinity and zooplankton [**I**]. abundance; [**II**].Shannon diversity index (H'), in vegetated and unvegetated habitats in LFN and LLT. Regression analyses indicate the relationship in (G). vegetated habitat at LLT to be statistically significant but not the other relationships. Only equation for the significant relationship shown.

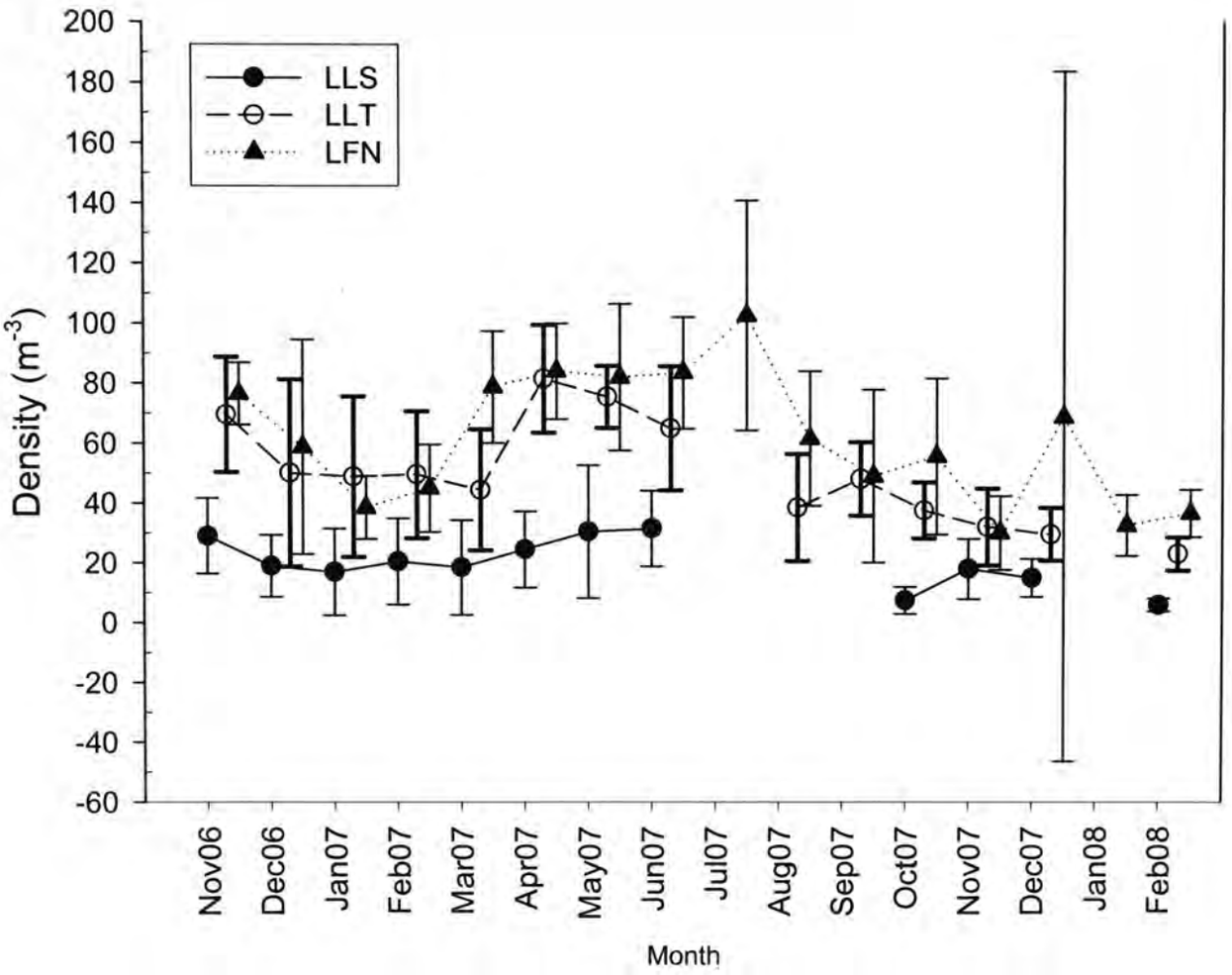


Fig. 2.31 Temporal change in mean (± S.D.) seaweed density in LLS, LLT and LFN over the sampling period from November 06 to February 08. Results of Friedman test results (Chi-square = 19.500, df = 2, $p<0.001$) indicate significant difference in seaweed density among sites.

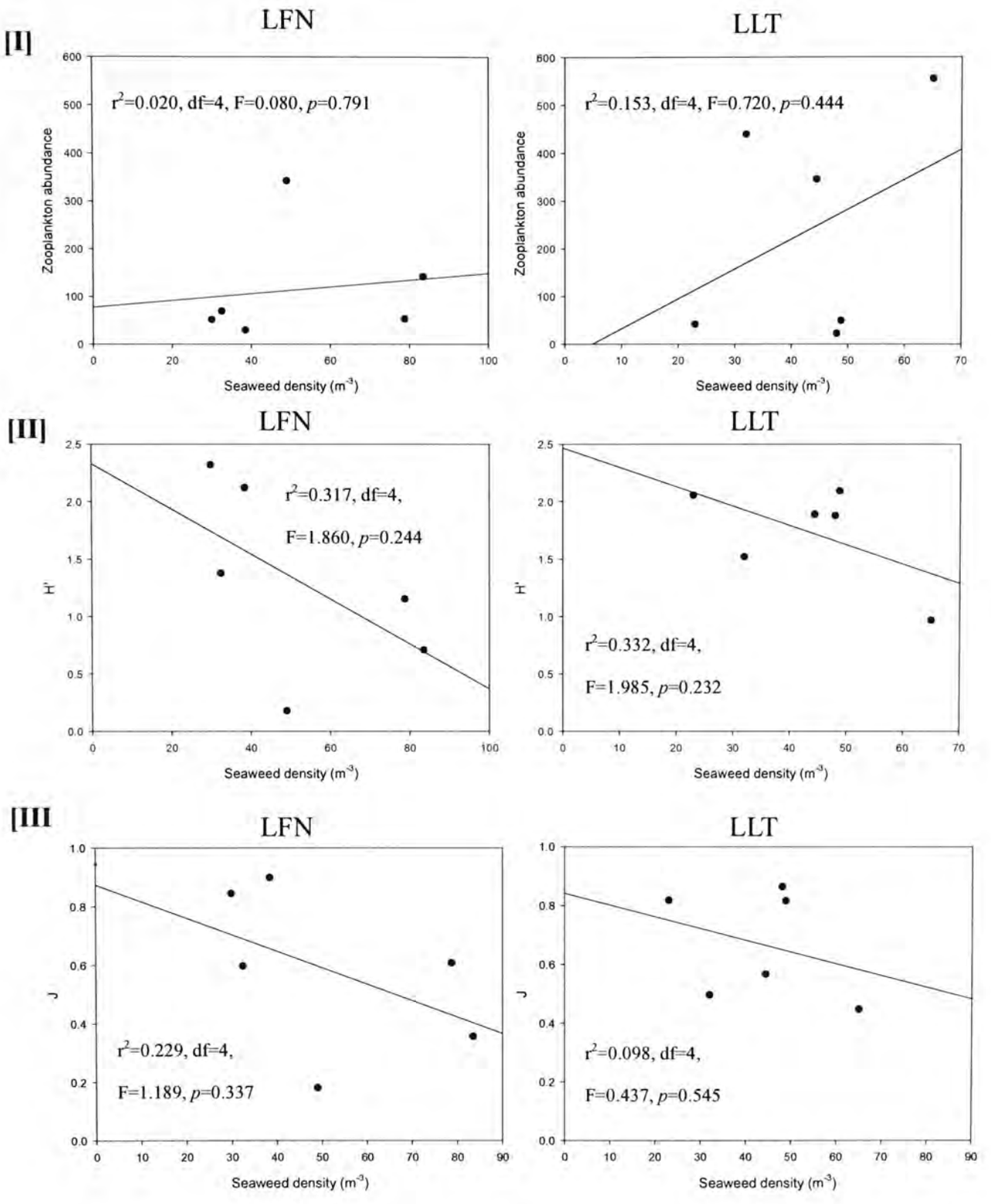


Fig. 2.32 Relationship between seaweed density and zooplankton [**I**]. abundance; [**II**].Shannon diversity index (H'); [**III**]. Evenness index (J), in LFN and LLT. Regression analyses indicate all relationships to be not statistically significant. Regression equations not shown.

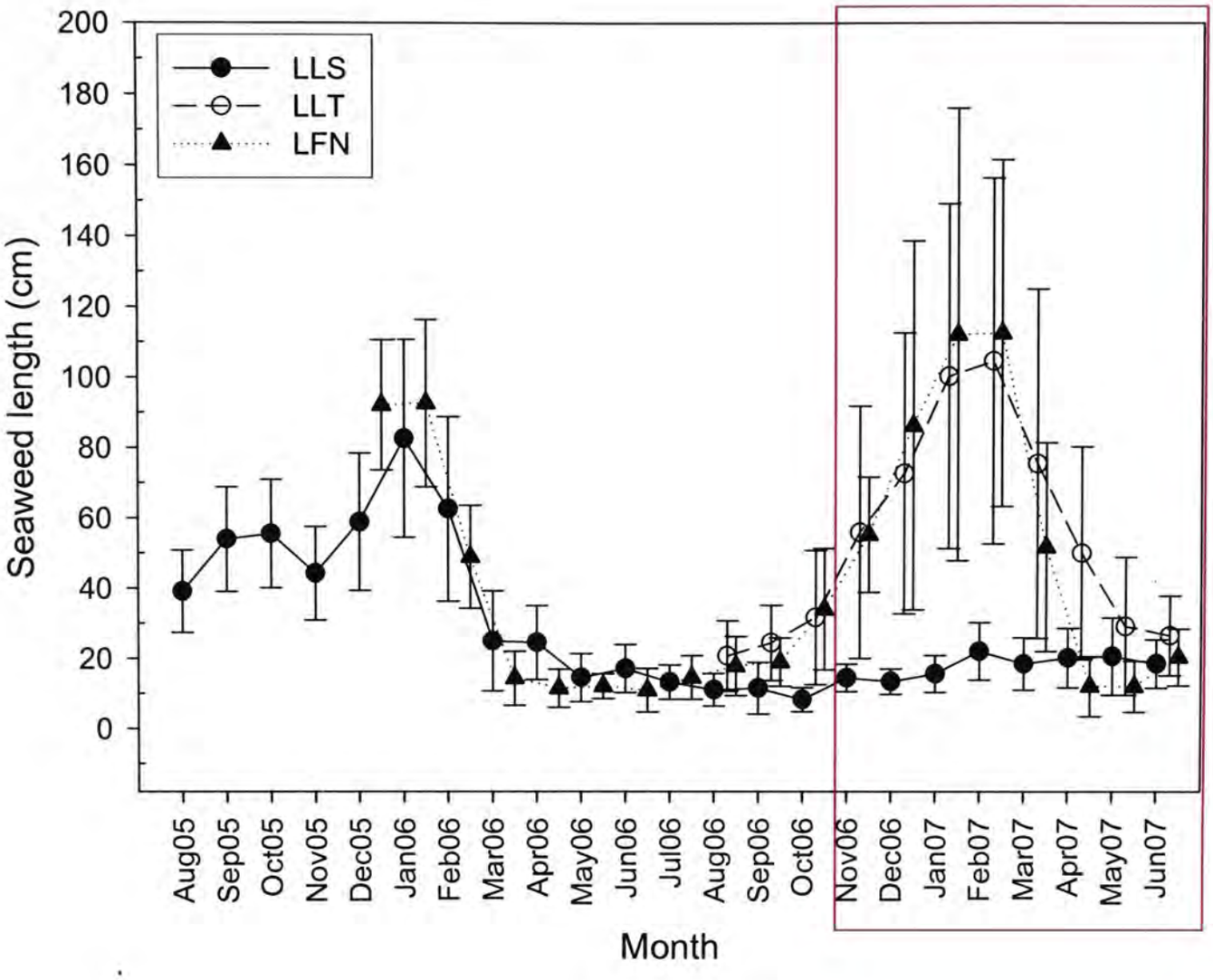


Fig. 2.33 Temporal change in mean (± S.D.) seaweed length in LLS, LLT and LFN from August 05 to June 07. Friedman test result (Chi-square = 7.750, df = 2, p = 0.021) showed significant difference in seaweed length among sites from November 07 to June 07.

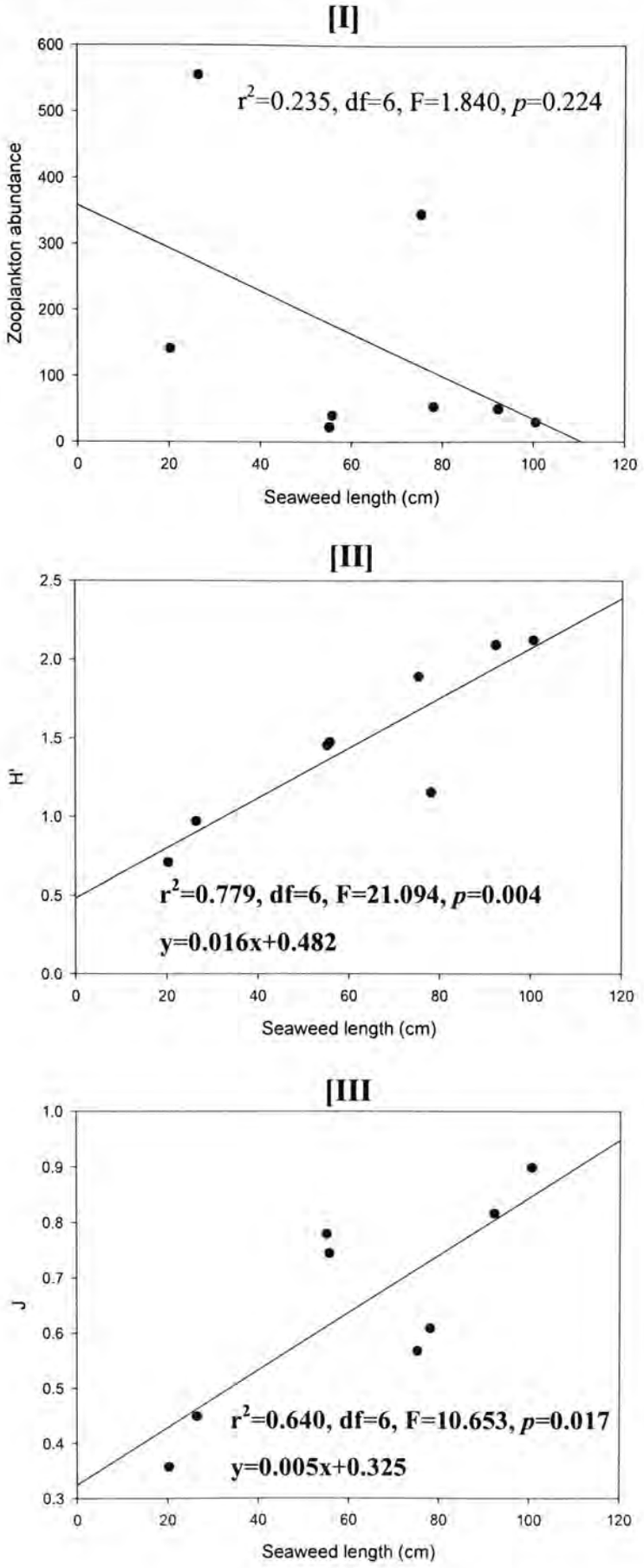


Fig. 2.34 Relationship between seaweed length and zooplankton [**I**]. abundance; [**II**]. Shannon diversity index (H'); [**III**]. Evenness index (J), in both LFN and LLT from November 06 to June 07. Regression analyses indicate relationships between seaweed length and H' as well as J to be statistically significant. Only equations for the significant relationship shown.

Chapter 3

Effects of Seaweed Canopy on the Structure of Zooplankton Assemblage in the *Sargassum siliquastrum* Bed

3.1 Introduction

The canopy-forming macroalgae and seagrass affect the structure of the associated faunal assemblages by modifying physical factors, such as living space (Jones *et al.* 1997, Crooks 2002), or by altering the biotic factors, such as density or foraging efficiency of predators (Menge 1978, Leber 1985, Eckman and Duggins 1991, Gagnon *et al.* 2003). Moreover, the dense canopy can dampen waves and influence hydrodynamic regimes (Duggins *et al.* 1990, Ackerman and Okubo 1993) and thus enhance the associated processes of sedimentation (Eckman *et al.* 1989, Duggins and Eckman 1994). By slowing down the water flow, the vegetative canopy acts as the site of larvae retention and recruitment, such as in the case of the economically important red drum *Sciaenops ocellatus* (Velimirov and Griffiths 1979, Kennelly 1989, Duggins *et al.* 1990, Rodriguez *et al.* 1993, Rooker and Holt 1997, Pakhomov *et al.* 2002).

Previous literatures reported the importance of canopy to the macrofaunal assemblage, with lower abundance and species diversity found in the canopy-removed habitat than in the vegetated habitat in intertidal zone (Bertness *et al.* 1999, Jenkins *et al.* 1999, Lee *et al.* 2001) as well as in subtidal environment (Graham 2004, Schmidt and Scheibling 2007, Vanella *et al.* 2007). In addition to loss of biodiversity, canopy removal also led to a series of unanticipated devastating impact on the marine food chain as well as the associated terrestrial food chain (Duggins *et al.* 1989, Bustamante and Branch 1996, Delille *et al.* 1997, Estes *et al.* 1998, Mann 2000, Pakhomov *et al.* 2002, Graham 2002, 2004). On the other hand, Connolly (1994, 1995) showed that the seagrass *Zostera muelleri* canopy was not the only overriding difference, at least over short periods, between patches with and without eelgrass in shaping the abundance and diversity of the associated epifaunal invertebrate and fish assemblages. Other factors, such as different structuring complexity and presence of the root/rhizome mat in some seagrass species, were also important in structuring the associated faunal assemblages.

Increased substratum complexity has been shown to promote higher abundance and diversity of zooplankton (Alldredge and King 1977, Porter *et al.* 1977, Jacoby and Greenwood 1988, Boström and Bonsdorff 2000). In Chapter 2, the seaweed bed of

Sargassum siliqaustrum was shown to harbour higher abundance and species diversity of zooplankton when compared with the unvegetated patches. However, the effect of canopy on zooplankton assemblage is poorly studied worldwide, in contrast to studies of canopy removal on epiphytic faunal assemblage previously mentioned. To confirm the findings in Chapter 2, the complexity offered by the vegetative structures, in particular the dense canopy during the rapid growth, reproductive stages of *Sargassum siliquastrum*, was studied in details in this chapter. The hypothesis being tested was that if the seaweed canopy is important to zooplankton community, treatment patches from which the canopies have been eliminated should support lower abundance and diversity of zooplankton than the control patches with canopies left intact. Furthermore, if the presence of seaweed canopy is the main cause for the significant difference in the zooplankton assemblages between vegetated and unvegetated habitats, then zooplankton assemblages associated with treatment patches should match those from the unvegetated patches.

3.2 Materials and Methods

3.2.1 Sample collection

Zooplankton samples were collected in Lung Lun Tsui (LLT) from three habitat types each marked an area of 3 x 2 m^2 in size. These included (a). Control (C), where seaweeds were kept in their natural state with their canopy in tact; (b). Treatment (T), where seaweed canopies were removed in the whole area by cutting the seaweeds half way through their stipes (about 100 cm); (c). Unvegetated (UNV) habitat, the nearest unvegetated patch to the treatment plots at comparable water depth. For the first two habitat types, two replicates of each type (i.e. C1 and C2; T1 and T2) were assigned in a random block design along the coast. Zooplankton net of 335 μm mesh size with a ring radius of 15 cm across the net opening was hauled close to the substratum (i.e. upper level of the canopy in vegetated habitat or barren ground made up of boulders in unvegetated habitat) for a distance of 17 m along the diagonals and boundaries of each experimental area. Net trawling was performed three times in each replicate of each habitat type. In total, 15 samples were collected each time: six (3 x 2) each from control and treatment habitats and three from unvegetated habitat. After each haul, the net was emptied, rinsed with minimum amount of filtered seawater, and its content

preserved in 35% formalin solution in white sampling bottles. Sample collection was performed on 4 dates in December 2007 (i.e. during the rapid growth stage of *Sargassum siliquastrum* when the canopies were dense): Day 0 (i.e. before removal of canopy in treatment habitats), and Days 1, 14 and 30 after treatment. Data were not collected immediately after the removal of canopy in treatment habitats in Day 0 in order to avoid any effect of disturbance due to cutting itself. However, due to persistent low underwater visibility, samples were only collected from one replicate of each control and treatment habitats on Day 1.

3.2.2 Data acquisition

All preserved zooplankton were identified to the possible lowest taxon level and counted using a dissecting microscope. Effort was focused on dominant groups of zooplankton. For certain taxa, further classification was done based on their life history stages, such as larvae, nauplii and adult.

Zooplankton density was expressed as numbers of individuals per m^3 seawater filtered to allow comparisons between habitats. Species richness in this study referred to number of species and zooplankton taxonomic groups. Diversity was calculated and

expressed as species richness, Shannon Diversity Index H' and Species Evenness Index J. Averages of density, species richness, H' and J were reported with standard deviation. The replicate data of species richness, H' and J for each habitat on each sampling date were subsequently pooled as no significant difference in species richness between replicates in each respective habitat type was detected (*t*-test: $p>0.05$). The proportional abundance of the most common zooplankton groups collected from different habitats was compared by calculating percentage of individuals belonging to the same taxonomic group over the total number of individuals. Association degree of the common groups was obtained by calculating the mean percentage of number of individuals in each habitat type in proportion to the total abundance of that group in the three habitats:

$$\text{Association degree of taxon N in C, T or UNV habitat (\%)} = \left(\frac{\text{\# N (in C, T or UNV habitat)}}{\text{Total \# of N in the three habitats}} \right) (100)$$

3.2.3 Data analysis

Throughout the whole course of sampling, a total of 21 zooplankton samples were each obtained from the control and treatment habitats while nine samples were collected from the unvegetated habitat for data analyses. All statistical analyses were

performed using SPSS 13.0 for Windows (SPSS Inc., USA). All data were tested for normality by Kolmogorov-Smirnov test or homogeneity of variance by Levene Median test. Transformation of the data was carried out if the parametric assumptions were not met. Non-parametric analyses were used instead if transformations of data still failed to satisfy the assumptions of parametric tests. The significance level (*p* value) of all statistical analyses was set at 0.05.

To compare the temporal change and among-habitats (i.e. C, T and UNV) difference in zooplankton density, species richness, H' and J, either parametric one-way ANOVA or non-parametric Kruskal-Wallis test was performed. Tukey post-hoc test was performed if ANOVA result was significant in order to identify between group difference. In all comparisons of zooplankton density, species richness, H' and J, and for all data calculation on proportional and association degree of zooplankton groups, data from Day1 were excluded due to incomplete sampling.

Temporal variations in zooplankton community structure among habitats, in terms of zooplankton abundance and species composition, during Days 0, 1, 14 and 30 were evaluated using non-metric multidimensional scaling ordination (MDS) and cluster analysis in PRIMER 6, based on the Bray-Curtis similarity measure, followed by

Simprof test using 1000 permutations to evaluate significant clusters in the dendrogram generated (Clarke and Warwick 2006). ANalysis Of SIMilarities (ANOSIM) was used to test the statistic for significant differences ($p<0.05$) between groups and their discriminating taxa were identified using the SIMilarity of PERcentages (SIMPER) routine in PRIMER 6. Abundance data were standardized and fourth-root transformed prior to the analyses in order to reduce the effect of overdominating species on the data set.

3.3 Results

3.3.1 Effects of Canopy on Zooplankton Community Structure

A significant among-habitat (i.e. Control, Treatment and Unvegetated) difference in zooplankton community structure was detected (Figure 3.1 A) on different sampling dates, revealing significantly distinct grouping of zooplankton assemblages based on habitat type and sampling time. The zooplankton community structure in each habitat type exhibited a uni-directional shift with sampling time (Figure 3.2). At a similarity level of 50%, two statistically significant clusters were grouped (Figure 3.1 B), in which one group was made up mainly of Day0 and Day1 samples while another of

Day14 and Day30 samples. Day0 and Day1 control samples were grouped with treatment samples of the corresponding days at about 70% level of similarity. Day14 and Day30 control samples were similar to each other at a similarity level of 70%; whereas one Day14 treatment sample clustered with Day30 unvegetated sample at around 55% similarity. while another Day14 treatment sample was distinctly separated from all other samples. Day30 treatment samples formed statistically significant cluster with each other at 80% similarity and grouped significantly with Day30 unvegetated sample at a similarity level of about 70%. This clustering pattern indicated that treatment samples showed a progressive increase in similarity with unvegetated samples in later sampling time (i.e. on Day14 and Day30) while control samples became distinctly different from treatment and unvegetated samples over the same period. Besides, zooplankton community structure in treatment habitat was in between those in control and unvegetated habitats on Day14 and Day30 but not on Day1 (Figure 3.2). Based on SIMPER analyses, the major discriminating taxa between control and unvegetated samples on Day14 were the gammaridean juvenile, while those between treatment and unvegetated samples were the calanoid *Acartia erythrae*, the gammaridean and the mysid juveniles. On Day30, the gammaridean amphipod was the principal differentiating taxon between control and unvegetated samples; whereas the gammaridean amphipod and the sergestid *Acetes japonica* were

the differentiating taxa between treatment and unvegetated samples. An increasing disparity in zooplankton assemblage between control and treatment samples with sampling time was further supported by the increasing magnitude of pairwise-r values in ANOSIM between control and treatment samples on Day14 and Day30 (Table 3.1).

3.3.2 Comparison between Control, Treatment and Unvegetated Habitats in terms of Zooplankton Abundance and Its Temporal Variation

Zooplankton abundance in control, treatment and unvegetated habitats responded to time in a similar manner but in varying magnitudes (Table 3.2). Zooplankton density significantly varied with sampling time in control and treatment (ANOVA: df=8, $p<0.05$) but not in unvegetated habitats (Kruskal-Wallis test: df=2, $p>0.05$) (Figure 3.3). In general, zooplankton density in all habitat types reached its minima on Day14 while attaining its maxima on Day30.

On Day0, that is, before the seaweed canopies in each habitat type were manipulated, zooplankton density in T2 at 141.13 ± 20.82 ind. m^{-3} and in unvegetated habitat at 165.33 ± 174.70 ind. m^{-3} were considerably higher than that in the other habitats at about 50 ind. m^{-3}. These zooplankton densities were, however, not significantly

different among habitats (Kruskal-Wallis test: Chi-square= 5.746, df= 4, $p>0.05$). On Day14, a significant difference in zooplankton density among habitats was detected (ANOVA: F= 4.071, df= 14, $p<0.05$). Tukey *post-hoc* test showed T1 to be significantly different from C1, while C2, T2 and unvegetated (UNV) were not different from either T1 or C1. Mean (± S.D.) zooplankton density in C1 at 30.81 ± 9.46 ind. m^{-3} was significantly the highest while that in T1 at 11.10 ± 9.46 ind. m^{-3} was the lowest. On Day30, zooplankton density was significantly different among habitats (ANOVA: F= 6.609, df= 14, $p<0.05$) and this was due mainly to the high zooplankton density in C1 and T1 at about 230 ind. m^{-3} and the low density in UNV at 77.15 ± 17.65 ind. m^{-3}.

3.3.3 Comparison between Control, Treatment and Unvegetated Habitats in terms of Zooplankton Species Composition and Its Temporal Variation

A total of 66 zooplankton taxa were identified in control, treatment and unvegetated habitats over the sampling period (Table 3.2). Figure 3.4 illustrates the temporal change in species richness in control, treatment and unvegetated habitats. Zooplankton species richness in the three habitat types changed with time in similar manner. The values diminished since Day0 and the lowest points were reached on

Day14. All habitat types experienced a drastic increase in species richness since Day14 and their greatest points were attained on Day30. However, only the species richness in control and treatment habitats exhibited a statistically significant temporal variation (ANOVA: df=17, $p<0.05$). From Day0 to Day14, the rate of decline in species richness in control was more steady than that in treatment habitats; whereas from Day14 to Day30, the rate of increase in species richness in control was more rapid than that in treatment habitats. On Day0, the mean (± S.D.) species richness in samples from control and treatment habitats at about 13 was considerably higher than those in unvegetated habitat at 10.33 ± 5.69, though no significant difference in species richness among habitats was detected (ANOVA: F= 0.322, df= 14, $p>0.05$). On Day14, species richness in control habitat at 12.33 ± 4.46 was noticeably greater than that in treatment and unvegetated habitats at about 8, but again no statistically significant difference in species richness among habitats was obtained (ANOVA: F= 1.914, df= 14, $p>0.05$). On Day30, a significant difference in zooplankton species richness among habitat types was found (ANOVA: F= 6.908, df= 14, $p<0.05$). Tukey post-hoc test showed two distinct groups among the habitat types: treatment and unvegetated vs. controls. Species richness in control habitat was significantly the highest at 25.33 ± 4.72, whereas that in treatment and unvegetated habitats was at a similar level of about 17.

The pattern of change in Shannon Diversity Index (H') was dissimilar with that in species richness (Figure 3.5). The trend of change in H' with time in samples from control and unvegetated habitats was similar: H' increased from Day0 to Day14 and remained relatively constant during Day14 to Day30. On the other hand, the value of H' in treatment samples declined with time and hit its minimum on Day30 at 1.49 ± 0.35. Temporal variation of Evenness Index (J) in different habitat types was similar to one another: J rose from Day0 to Day14 and dropped to a lower value from Day14 to Day30. On Day0, the highest H' was that from control habitat at 2.05 ± 0.32, followed by that from treatment habitat at 1.72 ± 0.35. The lowest value was that from unvegetated habitat at 1.57 ± 0.29. There was no statistically significant among-habitat differences in H' (ANOVA: F= 2.572, df= 14, $p>0.05$) as well as in J (Kruskal-Wallis test: Chi-square= 1.133, df= 2, $p>0.05$). On Day14, H' value significantly deviated among habitat types (ANOVA: F= 3.931, df= 14, $p<0.05$), with H' in control sample at 2.21 ± 0.33 being the greatest and that in treatment sample at 1.68 ± 0.36, the lowest. There was no significant difference in J among habitats on Day14 (Kruskal-Wallis test: Chi-square= 3.750, df= 2, $p>0.05$). On Day30, significant among-habitat differences in H' (Kruskal-Wallis test: Chi-square= 11.025, df= 2, $p<0.05$) and J (Kruskal-Wallis test: Chi-square= 8.225, df= 2, $p<0.05$) were detected. H' value at 2.21 ± 0.09 in control samples was significantly the highest, followed by

1.84 ± 0.12 in unvegetated samples and then the lowest value at 1.49 ± 0.35 in treatment samples. The maximum J value was obtained in control habitat at 0.69 ± 0.05, with the minimum in treatment habitat at 0.51 ± 0.10. There was no significant temporal difference in H' obtained in each of these three habitat types (ANOVA: df=17 [control and treatment]; df=8 [unvegetated], $p>0.05$) so data from all sampling days in each habitat were pooled and comparison for among-habitat difference showed H' to be significantly different (ANOVA: F= 14.618, df= 44, $p<0.05$). Tukey post-hoc test revealed two distinct groups among the habitat types: treatment and unvegetated samples belonged to one group that was different from the control. Significant difference in J with time was spotted in both control and treatment (Kruskal-Wallis test: df=2, $p<0.05$ for control; ANOVA: df= 2, $p<0.05$ for treatment) but not in the unvegetated habitats.

On Day0, species composition in control and treatment habitats was similarly more complex than that in unvegetated habitat (Figure 3.6). This pattern was consistent with that shown in Figure 3.4 in which species richness in control and treatment samples was considerably higher. The most common zooplankton groups in control and treatment habitats were the calanoid copepods (accounting about 50% of the total population) and the Lophogaster *Lophogaster pacificus* (around 10%); while those in

unvegetated habitats were the mysid juveniles (50%) and the calanoid copepods (15%). On Day14, species composition in the control habitat was relatively more complex than that in treatment and unvegetated habitats. The most dominant groups were calanoid copepods (accounting 30% of total population), gammaridean amphipods (11%), their juveniles (15%), and Lophogaster *Lophogaster pacificus* (10%); while the most common groups in samples from treatment and unvegetated habitats were the calanoid copepods (40-55%) and the mysid juveniles (5-20%). On Day30, the species composition in control habitat was evidently more complex than that in treatment and unvegetated habitats (Figures 3.4 and 3.5), with its species richness being significantly higher. The most abundant groups in control habitats were calanoid copepods (contributing about 40% of the total population), gammaridean amphipods (10%), their juveniles (23%), and harpacticoid copepods (12%); whereas the most common groups in treatment and unvegetated habitats were calanoid copepods (around 70%).

Figure 3.7 illustrates the degree of association of common zooplankton groups in each habitat type on each sampling day. In the main, the zooplankton groups were progressively more associated with vegetation in control habitat on Day14 and Day30 after canopy removal. Gammaridean exhibited an increase in association with control

habitat from 50% on Day0 to 70% on Day14 and Day30. Macruran larvae were 50% associated with control habitat on Day0 while totally associated with it on Day14 and Day30. The association degree of Lophogaster *Lophogaster pacificus* with control habitat augmented from 40% on Day0 to 80% on Day14 and Day30. Sergestids were increasingly more associated with the control habitat, with the degree rose by 40% after canopy removal. Gastropod larvae were equally associated with control and treatment habitats on Day0 but were 100% associated with control habitat on Day14 and Day30. Molluscan larvae were entirely associated with treatment habitat on Day14 but with control habitat on Day30. Polychaetes and arrow worms were more associated with unvegetated habitat on Day0, while entirely associated with treatment habitat on Day14 and with control habitat on Day30. Some zooplankton groups were in overall more or totally associated with control habitat after canopy removal. Isopods and squid juveniles were entirely associated with control habitat. Gammaridean juveniles, caprellidean, cyclopoids, harpacticoids, mysids and their juveniles were generally more associated with control habitat on Day14 and Day30 than on Day0. On the contrary, some zooplankton groups were distributed regularly among different habitat types after canopy removal. Calanoids were increasingly associated with treatment habitat over the sampling time while fish juveniles and eggs were equally distributed among habitats across the same period. In details, after

canopy removal on Day14 and Day30, the fish species *Pelates quadrilineatus* and *Sebastiscus marmoratus* were only encountered in control but not in treatment habitats; while the fish larvae of Synodontidae were only found in unvegetated habitat (Table 3.2).

3.4 Discussion

3.4.1 Effects of Canopy Removal on the Zooplankton Assemblage Structure

In this study, the high similarity between control and treatment groups on Day1 in MDS plots and the corresponding dendrograms suggested that no immediate detectable impact on the overall zooplankton assemblage structure due to canopy removal was found. However, on Day14 and Day30, treatment samples showed a progressive similarity with unvegetated samples while control samples were distinctly separated from treatment and unvegetated samples. Therefore, the impact of canopy removal on zooplankton assemblage structure was not apparent immediately but became more obvious in later times. Connolly (1995) reported that macrofaunal species with slow emigration rates lingered on in canopy-removal habitat even if conditions were unfavourable for long-term survival. This is supported by the

response of zooplankton to canopy removal in this present study. This delay in zooplankton response might be related to the time taken for zooplankton to adapt to the changing environment because of their relatively less advanced sensory and locomotory mechanisms. Due to their diminished body size in order to avoid the detection of visual predators, the sensory organ of most net zooplankton is relatively less well developed, with only simple organs to detect light orientation (Hamner 1996). Additionally, these zooplankton possess weak swimming ability and move more slowly especially under turbid water conditions (Hwang *et al.* 1994, Haury and Yamazaki 1995).

The effect of canopy removal on zooplankton abundance was quite the opposite to that observed on the overall zooplankton community structure. The present data showed that zooplankton density was significantly the lowest in treatment habitat, and the highest in control habitat on Day14; while on Day30, zooplankton density in treatment and control habitats was statistically similar but that in unvegetated habitat was significantly lower. The increased species diversity on Day30 was attributable to the higher abundance of zooplankton observed on the same day in treatment habitat. This trend of change in zooplankton abundance over time after canopy removal indicated that the removal of canopy might induce an immediate but short term

impact on zooplankton abundance. This inconspicuous treatment effect on zooplankton abundance might probably be the consequence of the mobile zooplankton moving back and forth in packs between treatment patch and the surrounding vegetated areas along with the waves and currents, as evidenced by the significant difference in zooplankton density between replicates of the same habitat type (*t*-test: $p<0.05$). The patchy distribution of zooplankton is intrinsic to zooplankton behaviour.

In the current study, the pattern of change in species richness in the three habitat types over time was similar, albeit in different magnitudes after canopy removal. From Day0 to Day14, species richness in control habitat gently dropped while that in treatment habitat showed a more rapid decline. However, from Day14 to Day30, the rate of increase in species richness in control habitat was more rapid than that in treatment habitat, indicating that the increase in species richness in the seaweed bed might be hindered by canopy removal. Moreover, after canopy removal, species richness in control habitat was evidently the highest among the habitat types; while both treatment and unvegetated habitats harboured statistically similar low species richness. Thus, vegetated habitat with canopy might provide a relatively more stable environment in maintaining species richness and canopy removal may cast a

long-lasting destructive impact on its zooplankton species diversity.

3.4.2 Role of Seaweed Canopy in Zooplankton Community and the Potential Impacts of Canopy Removal on Coastal Ecosystem

Selection of algal habitats by mobile macrofauna is likely regulated by the different shelters offered by the three dimensional-structured macroalgae (Schmidt and Scheibling 2007), as well as biotic mechanisms, such as feeding mode and trophic interaction among members of the macrofauna (Hicks 1980, Pakhomov *et al.* 2002, Jara 2005). This results in the close association of zooplankton species with specific substratum structure. In the present study, after canopy removal, zooplankton groups, namely gammaridean and their juveniles, macruran larvae, lophogaster *Lophogaster pacificus*, sergestids, gastropods and molluscan larvae, became increasingly associated with the control habitat where the canopy remained intact. In addition, some zooplankton taxa, such as isopods, squid juveniles, caprellidean, cyclopoids, harpacticoids, mysids and their juveniles, as well as the fish species *Pelates quadrilineatus* and *Sebastiscus marmoratus*, were solely associated with canopy in the control habitat. This indicated a specific preference on seaweed canopy by certain zooplankton taxa. The close association of particular zooplankton fauna with canopy

might be the consequences of three possible reasons. Firstly, the vegetative canopy acted as an ample source of food to a variety of zooplankton at different trophic levels, such as the detritus-feeders harpacticoids and mysids (Liu and Wang 2000, Coman *et al.* 2003, Yang and Suen 2006), herbivorous isopods, gammaridean and caprellidean (Ren 2006, Yang and Suen 2006) and the carnivorous fish *Pelates quadrilineatus* and *Sebastiscus marmoratus* (Sadovy and Cornish 2000). The seaweed canopy was the main site of photosynthetic reactions and constituted the main bulk of the macroalgal biomass (Middelboe and Binzer 2004). This huge biomass could exert a positive influence on the species richness of the zooplankton assemblage, as in the case of the associated macrofauna (Ingólfsson 1995, Albertoni *et al.* 2001, Danovaro and Fraschetti 2002), by the provision of tremendous amount and diversity of food, e.g. phytodetritus, bacteria, epiphytic microscopic algae, the understorey algae species, (Kennelly 1989, Connolly 1995, Jenkins *et al.* 1999, Lee *et al.* 2001, Graham 2004) as well as the associated invertebrates (Connolly 1994). Secondly, dense canopy can dampen waves (Duggins *et al.* 1990, Ackerman and Okubo 1993) and thus enhance the associated sedimentation processes (Eckman *et al.* 1989, Duggins and Eckman 1994), thereby creating a hydrodynamically stable environment with abundant supply of suspended particulates for filter-feeders, such as copepods, mysids and other invertebrate larvae. This phenomenon of stabilized hydrology was further confirmed

by the current data that zooplankton distribution was significantly more even in control than in treatment habitats after canopy removal. Thirdly, the complex-structured canopy could create a variety of refuges and microhabitats for zooplankton close to the surface water to stay away from predators (Leber 1985, Vanella *et al.* 2007).

Marine vegetation was shown to facilitate the retention of invertebrate and fish larvae, thus their recruitment and settlement within the bed (Ekman 1983, 1987, Eckman and Duggins 1991, Irlandi and Peterson 1991, Ray and Stoner 1995, Jenkins and Sutherland 1997, Rooker and Holt 1997, Bologna and Heck 1999, Boström and Bonsdorff 2000, Lamare and Barker 2001, Pakhomov *et al.* 2002, Epifanio *et al.* 2003, Gamfeldt *et al.* 2005, Pershing *et al.* 2005, King and Sheridan 2006, Vanella *et al.* 2007). Bell *et al.* (1987) found a total of 52 fish species larvae that settled in the artificial seagrass canopy model but not in places without shelters. Besides, Nelson (2001) reported the initial recruitment of kelp rockfish, *Sebastes atrovirens*, to the canopy of the giant kelp, *Macrocystis pyrifera*, along the coast of central California. Moreover, complete loss of the abundance and diversity of the canopy fish assemblage was discovered to be associated with the disappearance of the kelp canopy, their primary habitat (Graham 2004, Vanella *et al.* 2007). Most critically, macroalgal

canopy is believed to be vital in nurturing fishery resources of economic importance, e.g. the Japanese mariculture species *Sebastiscus marmoratus* (Sadovy and Cornish 2000). Our present data similarly pointed to the function of the *Sargassum siliquastrum* canopy as site of larvae retention and nursery grounds, as evidenced by the intimate association of the invertebrate and fish larvae, as well as squid juvenile, with the seaweed canopy.

Being an indispensable component in maintaining the zooplankton species diversity, removal of seaweed canopy can cause loss of certain associated species. This might in turn give rise to the collapse of the food chain. A top-down trophic cascade was illustrated in previous studies that the disappearance of kelp canopy-associated fish preceded the onset of episodic amphipod and urchin grazing outbreaks that can cause local giant kelp deforestation (Estes *et al.* 1998, Graham 2002, 2004). Deforestation can lead to further loss in biodiversity and unexpected influence on the macroalgae community, with a further impact on the linked terrestrial food chain as phytodetritus served as a food source to the coastal fauna (Duggins *et al.* 1989, Bustamante and Branch 1996, Delille *et al.* 1997, Pakhomov *et al.* 2002). However, no subsequent collapse of food chain due to canopy removal was noticeable in the current study, further loss in biodiversity and impact on the associated marine food chain, together

with the linked terrestrial food chain, cannot be ruled out.

3.5 Summary and Conclusion

The *Sargassum siliquastrum* canopy appears to provide its associated zooplankton with ample supply of food due to its high biomass productivity and a refuge of stabilized hydrodynamic environment. Hence, the removal of this canopy resulted in an impact on the zooplankton assemblage structure, as evidenced by its change in canopy removed treatment samples showing a progressive similarity with unvegetated samples while becoming distinctly different from the controls. The removal of canopy induced an immediate but not long-lasting decline in zooplankton abundance. In contrast, canopy removal exerted a comparatively long-lasting negative impact on zooplankton species diversity. Effect of canopy removal on zooplankton species richness was more devastating than that on its abundance. This is consistent with the findings earlier (Chapter 2) that difference in species richness was probably the main reason causing distinct difference in zooplankton assemblage structure between vegetated and unvegetated habitats. With zooplankton species richness in treatment and unvegetated habitats becoming statistically similar after canopy removal, the role of seaweed canopy in structuring the zooplankton species diversity in vegetated and

unvegetated habitats is evident.

The canopy of *Sargassum siliquastrum* serves as a site for larval retention and as larval nursery grounds. Removal of seaweed canopy can lead to the loss of certain associated species. While no subsequent collapse of the food chain and deforestation was apparent in the present study, further loss in biodiversity and impact on the associated marine food chain, together with the linked terrestrial food chain, cannot be ruled out. Additional ecological consequences of canopy removal should be explored, especially given that canopy removal has been the strategy used in the harvesting of many canopy forming species, in order to maintain sustaining exploitation of these seaweed resources.

Table 3.1 Results of Pairwise ANOSIM comparing the zooplankton assemblages between control (C), treatment (T) and unvegetated (unv) habitat in each sampling day (all values, $p>0.05$).

Pairwise ANOSIM										
	Day0-C	Day0-T	Day0-unv	Day1-C	Day1-T	Day14-C	Day14-T	Day14-unv	Day30-C	Day30-T
Day0-C										
Day0-T	0									
Day0-unv	1	1								
Day1-C	1	0	\							
Day1-T	0	0	\	\						
Day14-C	1	1	1	1	1					
Day14-T	0.5	0.25	1	0	0	0.25				
Day14-unv	1	1	\	\	\	1	-1			
Day30-C	1	1	1	1	1	1	0.5	1		
Day30-T	1	1	1	1	1	1	0	1	0.75	
Day30-unv	1	1	\	\	\	1	-1	\	1	1

Table 3.2 The mean (± S.D.) abundance (no. of individuals) of each zooplankton taxonomic group in control, treatment and unvegetated habitats (with replicates) on each sampling day.

Taxonomic groups	Day 0 (Pre-impact)					Day 1		Day 14					Day 30				
	Control 1	Control 2	Treatment 1	Treatment 2	unvegetated	Control 1	Treatment 1	Control 1	Control 2	Treatment 1	Treatment 2	unvegetated	Control 1	Control 2	Treatment 1	Treatment 2	unvegetated
Amphipoda																	
Gammaridean																	
Synopiidae	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	2.33 ± 1.53	2.00 ± 1.00	0.33 ± 0.58	1.67 ± 1.15	0.00 ± 0.00	15.67 ± 3.21	15.00 ± 2.65	8.00 ± 3.61	4.67 ± 1.53	0.00 ± 0.00
Maxillipidae	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Talitridae	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.33 ± 2.31	0.33 ± 0.58	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00
Stenothoidae	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.33 ± 1.53	0.67 ± 1.15	1.00 ± 1.00	0.00 ± 0.00	0.00 ± 0.00	3.00 ± 2.65	3.00 ± 1.00	0.00 ± 0.00	0.67 ± 0.58	0.00 ± 0.00
Gammaridea juvenile	0.67 ± 0.58	0.67 ± 1.15	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.33 ± 0.71	4.33 ± 0.58	5.33 ± 1.53	0.00 ± 0.00	1.67 ± 2.89	0.00 ± 0.00	63.67 ± 14.01	39.00 ± 9.54	14.00 ± 6.24	22.33 ± 16.26	2.33 ± 2.52
Caprellidean	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.33 ± 1.53	0.33 ± 0.71	0.33 ± 0.58	0.33 ± 0.58	0.00 ± 0.00	1.00 ± 1.73	0.00 ± 0.00	0.67 ± 0.58	1.67 ± 1.53	0.67 ± 0.58	0.33 ± 0.58	0.33 ± 0.58
Decapoda																	
Brachyura larva	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.71	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58
Macrura larva	1.00 ± 1.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 1.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.67 ± 1.15	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Sergestidae, *Lucifer spp.*	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.67 ± 1.53	7.33 ± 6.66	0.67 ± 1.15	1.00 ± 0.71	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Acetes japonica	0.00 ± 0.00	1.33 ± 2.31	0.33 ± 0.58	0.67 ± 1.15	0.67 ± 1.15	0.33 ± 0.58	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	2.33 ± 3.21	2.00 ± 1.73	1.33 ± 1.15	3.00 ± 2.00	0.00 ± 0.00
Sergestidae larva	0.33 ± 0.58	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.33 ± 2.31	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Copepoda																	
Calanoida																	
Acartia erythrae	14.00 ± 6.08	14.67 ± 5.03	3.33 ± 2.31	61.33 ± 17.01	76.00 ± 80.85	3.00 ± 3.24	4.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	2.00 ± 2.00	7.00 ± 2.66	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.67 ± 0.58
Temora turbinata	5.00 ± 6.08	1.00 ± 1.00	1.00 ± 1.73	2.33 ± 2.52	31.00 ± 32.42	11.33 ± 12.86	6.67 ± 7.07	1.00 ± 1.00	0.00 ± 0.00	0.33 ± 0.58	0.33 ± 0.58	1.33 ± 2.31	3.33 ± 1.53	0.67 ± 0.58	2.67 ± 2.08	2.67 ± 1.15	1.33 ± 0.58
Subeucalanus subcrassus	0.00 ± 0.00	0.33 ± 0.58	1.33 ± 1.53	1.33 ± 0.58	2.00 ± 3.46	1.33 ± 2.31	0.33 ± 0.71	3.00 ± 4.36	0.00 ± 0.00	0.33 ± 0.58	0.67 ± 1.15	0.00 ± 0.00	4.67 ± 2.31	5.00 ± 4.94	4.00 ± 2.89	3.67 ± 2.15	5.00 ± 2.73
Pseudodiaptomus incisus	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	4.00 ± 5.29	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Labidocera minuta	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	3.33 ± 4.93	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Paracalanus parvus	7.33 ± 4.93	3.00 ± 2.65	4.00 ± 6.08	4.33 ± 1.53	1.67 ± 2.89	13.33 ± 12.74	6.00 ± 7.07	5.33 ± 6.11	5.67 ± 1.15	2.67 ± 1.53	8.33 ± 5.86	5.00 ± 2.00	97.33 ± 10.69	48.00 ± 16.52	206.00 ± 72.67	95.00 ± 34.22	46.67 ± 15.63
Paracalanus spp.	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.67 ± 1.15	0.67 ± 0.58	0.33 ± 0.58
Tortanus forcipatus	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.33 ± 0.58	1.67 ± 2.89	0.67 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Tortanus gracilis	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.33 ± 0.58
Undinula vulgaris	0.00 ± 0.00	0.67 ± 0.58	0.33 ± 0.58	0.33 ± 0.58	0.33 ± 0.58	4.00 ± 5.20	1.00 ± 0.71	1.33 ± 1.15	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	2.00 ± 2.10	0.33 ± 0.58	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00
Euchaeta spp.	0.33 ± 0.58	0.33 ± 0.58	1.00 ± 1.00	1.33 ± 2.31	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	1.00 ± 1.00	0.00 ± 0.00	1.33 ± 1.15	0.33 ± 0.58	0.33 ± 0.58	0.67 ± 0.58	0.33 ± 0.58	2.33 ± 1.15	2.33 ± 0.58	4.33 ± 0.58
Euchaeta concinna	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Calanopia elliptica	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.67 ± 1.15	0.00 ± 0.00	0.67 ± 1.15	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Centropages orsinii	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	1.67 ± 2.08	1.00 ± 1.00	1.67 ± 1.53
Centropages tenuiremis	0.33 ± 0.58	0.67 ± 1.15	0.33 ± 0.58	0.67 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.71	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.67 ± 0.58	1.00 ± 1.73	0.00 ± 0.00	0.00 ± 0.00	0.67 ± 1.15	0.67 ± 0.58
Centropages dorsispinatus	0.00 ± 0.00	0.33 ± 0.71	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Centropages longicornis	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Centropages spp.	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.33 ± 1.15	0.33 ± 0.58	0.33 ± 0.58	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00
Acrtideus armatus	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cyclopoida																	
Oithona rigida	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Oithona spp.	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 1.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	4.00 ± 2.00	4.67 ± 0.58	0.67 ± 1.15	1.67 ± 1.53	0.00 ± 0.00
Microsetella norvegica	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Corycaeus spp.	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.67 ± 2.89	0.00 ± 0.00	0.67 ± 1.15	0.00 ± 0.00	0.67 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.67 ± 1.15
Harpacticoida	0.67 ± 0.58	1.67 ± 2.08	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.67 ± 1.15	0.33 ± 0.71	0.33 ± 0.58	0.67 ± 1.15	0.00 ± 0.00	0.67 ± 0.58	0.00 ± 0.00	18.33 ± 13.32	33.67 ± 5.51	4.00 ± 3.00	5.33 ± 6.81	0.33 ± 0.58
Copepoda nauplii	0.67 ± 1.15	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

Table 3.1 (cont'd)

Taxonomic groups	Day 0 (Pre-impact)					Day 1		Day 14					Day 30				
	Control 1	Control 2	Treatment 1	Treatment 2	unvegetated	Control 1	Treatment 1	Control 1	Control 2	Treatment 1	Treatment 2	unvegetated	Control 1	Control 2	Treatment 1	Treatment 2	unvegetated
Fish larva																	
Synodontidae	0.00 ± 0.00	0.33 ± 0.58	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.67 ± 0.58
Pelates quadrilineatus	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Sebastiscus marmoratus	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Fish eggs	1.67 ± 0.58	0.33 ± 0.58	0.00 ± 0.00	1.00 ± 1.73	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.67 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.33 ± 1.15	0.67 ± 1.15	0.00 ± 0.00	2.67 ± 0.58	1.33 ± 0.58	2.00 ± 2.00
Isopoda adult	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.67 ± 0.58	0.33 ± 0.71	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Isopoda juvenile	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.67 ± 0.58	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mysidacea																	
Mysida																	
Siriella vulgaris	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.33 ± 0.71	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	2.00 ± 2.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Hypererythrops spinifera	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 1.00	0.67 ± 1.15	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00
Mysidae juvenile	0.33 ± 0.58	1.33 ± 1.15	0.00 ± 0.00	1.33 ± 0.58	0.00 ± 0.00	8.00 ± 5.57	2.67 ± 5.66	2.67 ± 3.79	1.33 ± 1.15	0.00 ± 0.00	2.33 ± 0.58	5.33 ± 2.89	5.67 ± 6.43	7.00 ± 1.73	0.33 ± 0.58	5.33 ± 4.16	4.00 ± 2.00
Lophogastrida																	
Lophogaster pacificus	4.00 ± 1.73	2.00 ± 2.10	9.67 ± 6.69	1.33 ± 1.73	0.00 ± 0.00	4.67 ± 4.62	2.00 ± 2.83	2.33 ± 2.66	1.67 ± 2.10	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	3.00 ± 2.68	2.33 ± 1.73	0.00 ± 0.00	1.33 ± 1.58	0.00 ± 0.00
Lophogastridae juvenile	1.33 ± 1.15	2.00 ± 1.73	3.00 ± 4.36	2.33 ± 3.21	0.00 ± 0.00	0.33 ± 0.58	0.67 ± 1.41	1.00 ± 1.00	0.67 ± 1.15	0.00 ± 0.00	1.00 ± 1.00	0.33 ± 0.58	2.00 ± 1.00	2.67 ± 1.53	0.33 ± 0.58	0.67 ± 1.15	0.00 ± 0.00
Mollusca																	
Squid juvenile	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 1.73	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Gastropoda, *Creseis acicula*	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Gastropoda unidentified larva	0.67 ± 1.15	1.00 ± 1.73	0.67 ± 1.15	1.33 ± 0.58	0.00 ± 0.00	1.33 ± 2.31	0.33 ± 0.71	0.67 ± 1.15	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 1.00	0.67 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Molluscus, Lamellibrachia larva	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Bivalvia unidentified larva	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 1.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Echinodermata unidentified larva	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58
Polychaeta larva	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	1.00 ± 1.00	3.00 ± 2.65	0.33 ± 0.58	1.00 ± 2.12	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	4.00 ± 1.00	3.33 ± 4.93	0.67 ± 1.15	0.67 ± 1.15	0.00 ± 0.00
Chaetognatha																	
Sagitta enflata	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	19.67 ± 24.42	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.67 ± 1.15	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Sagitta regularis	1.00 ± 1.00	1.00 ± 1.00	0.67 ± 1.15	2.33 ± 0.58	4.67 ± 8.08	2.33 ± 2.52	0.33 ± 0.71	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cirripedia larva	10.67 ± 4.62	10.33 ± 4.16	5.67 ± 3.51	21.67 ± 8.33	0.00 ± 0.00	6.33 ± 5.03	3.67 ± 6.36	4.33 ± 2.52	1.67 ± 2.08	5.00 ± 5.00	9.67 ± 4.04	3.33 ± 4.16	0.00 ± 0.00	0.00 ± 0.00	0.67 ± 0.58	1.33 ± 2.31	1.00 ± 0.00
Cladocera	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	10.33 ± 7.57	9.00 ± 4.36	33.00 ± 27.62	18.33 ± 8.02	15.00 ± 6.24
Cumacea	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.67 ± 1.15	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cnidaria																	
Hydroid polyp	1.00 ± 1.00	2.00 ± 1.73	0.67 ± 1.15	3.67 ± 1.53	1.00 ± 1.73	2.67 ± 3.06	1.67 ± 0.71	1.33 ± 1.15	1.00 ± 1.73	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.67 ± 0.58	1.67 ± 2.08	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58
Hydrozoa medusa	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	2.67 ± 2.08	0.67 ± 0.58	2.33 ± 1.53	1.33 ± 1.15	0.33 ± 0.58
Nemertea	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.67 ± 1.15	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.33 ± 0.58	3.33 ± 0.58	2.00 ± 1.00	0.33 ± 0.58	3.00 ± 1.73	3.33 ± 0.58
Oikopleura	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	4.33 ± 5.86	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.00 ± 1.00	0.00 ± 0.00	0.67 ± 0.58	3.00 ± 1.00	2.00 ± 2.00	2.33 ± 1.53	1.00 ± 0.00	1.67 ± 1.15
Others, e.g. insecta	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.33 ± 1.15	3.67 ± 6.35	0.67 ± 0.58	0.33 ± 0.71	0.33 ± 0.58	0.00 ± 0.00	0.33 ± 0.58	0.00 ± 0.00	0.67 ± 1.15	0.33 ± 0.58	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.58	0.67 ± 0.58
Total	52.33 ± 24.83	46.33 ± 22.59	33.33 ± 25.42	170.50 ± 23.69	165.33 ± 174.70	67.67 ± 61.26	51.50 ± 13.44	37.00 ± 11.36	26.00 ± 3.61	13.33 ± 5.86	33.33 ± 4.16	27.67 ± 10.15	266.00 ± 32.05	189.33 ± 31.09	289.33 ± 90.80	180.00 ± 53.11	94.33 ± 22.72

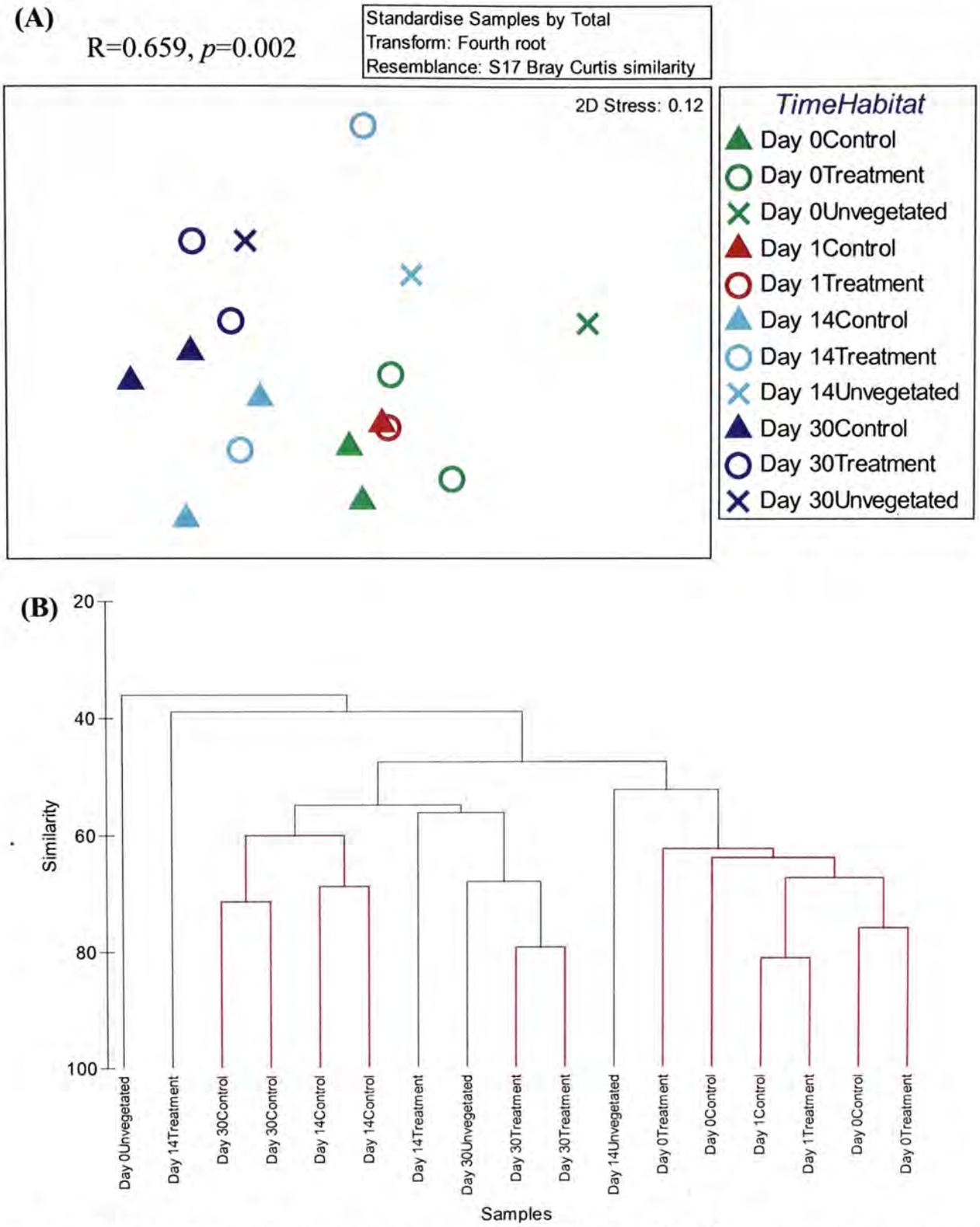


Fig. 3.1 (**A**). MDS ordination plot (stress = 0.12) and (**B**). Dendrogram based on Bray-Curtis similarity, fourth root transformed group average data showing the zooplankton assemblage in control, treatment and unvegetated habitats on each sampling day. Each point represents mean of triplicate zooplankton tows from each habitat on each day. Two sets of tow were made in control and treatment habitats while one set was carried out in unvegetated habitat each time. ANOSIM results (with Global-R = 0.659) indicate significant separation in the structure of zooplankton assemblages among groups of habitat on each sampling date. Solid lines in dendrogram display groupings which are statistically significant (Simprof test, $p<0.05$).

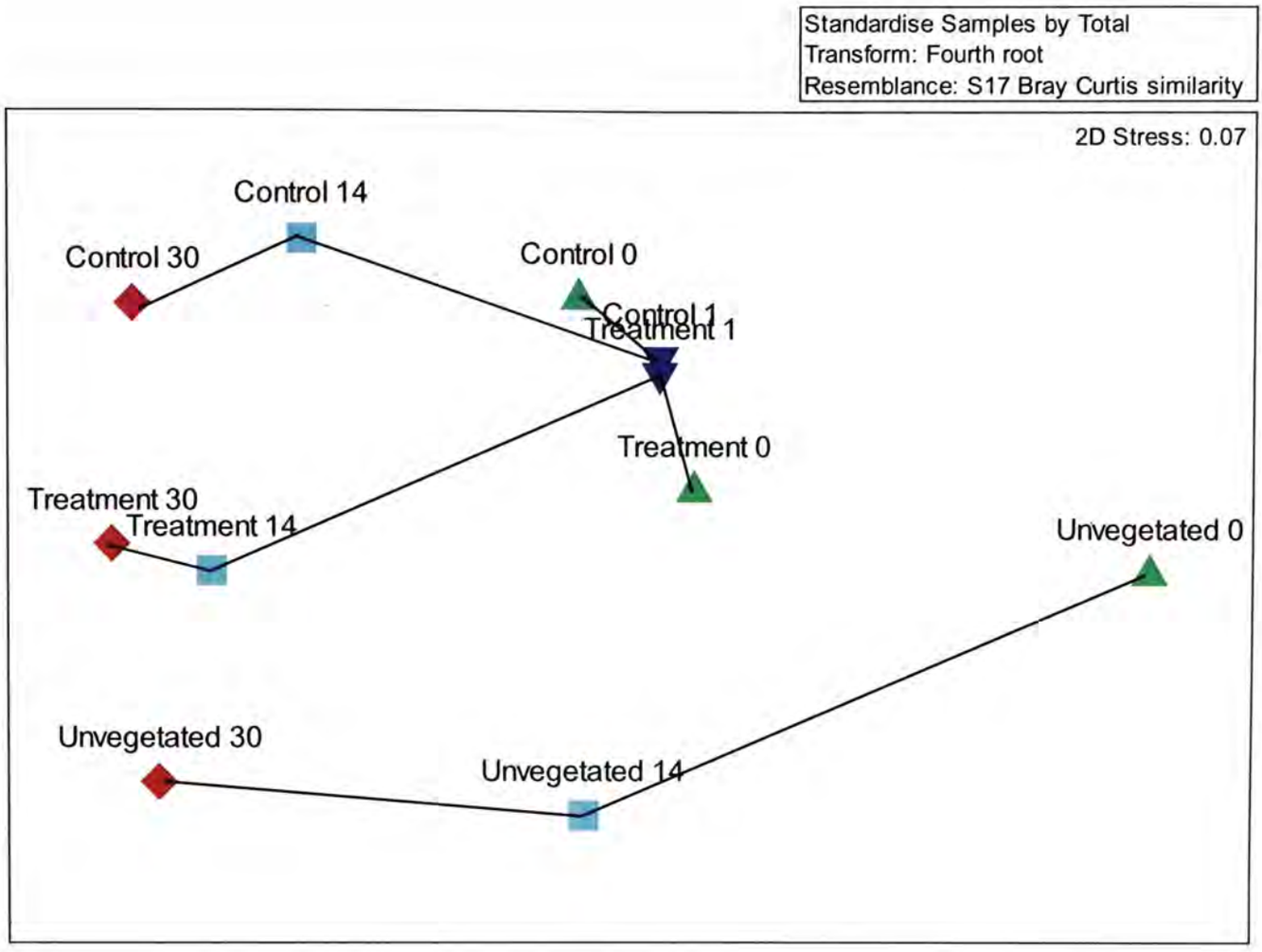


Fig.3.2 MDS ordination plot showing the temporal shift in zooplankton assemblage in control, treatment and unvegetated habitats (stress = 0.07). Each point represents mean of two sets of triplicate zooplankton tows from replicates of control and treatment habitats; or mean of triplicate zooplankton tows from unvegetated habitat on sampling days 0, 1, 14 and 30. Triplicate samples were only collected from one replicate of each control and treatment habitats on Day1.

Temporal change in zooplankton density

Control 1: ANOVA, F=77.655, df=8, p<0.001

Control 2: ANOVA, F=46.098, df=8, p<0.001

Treatment 1: ANOVA, F=23.982, df=8, p=0.001

Treatment 2: Chi-square=6.489, df=2, p=0.039

Unvegetated: Chi-square=2.489, df=2, p=0.288

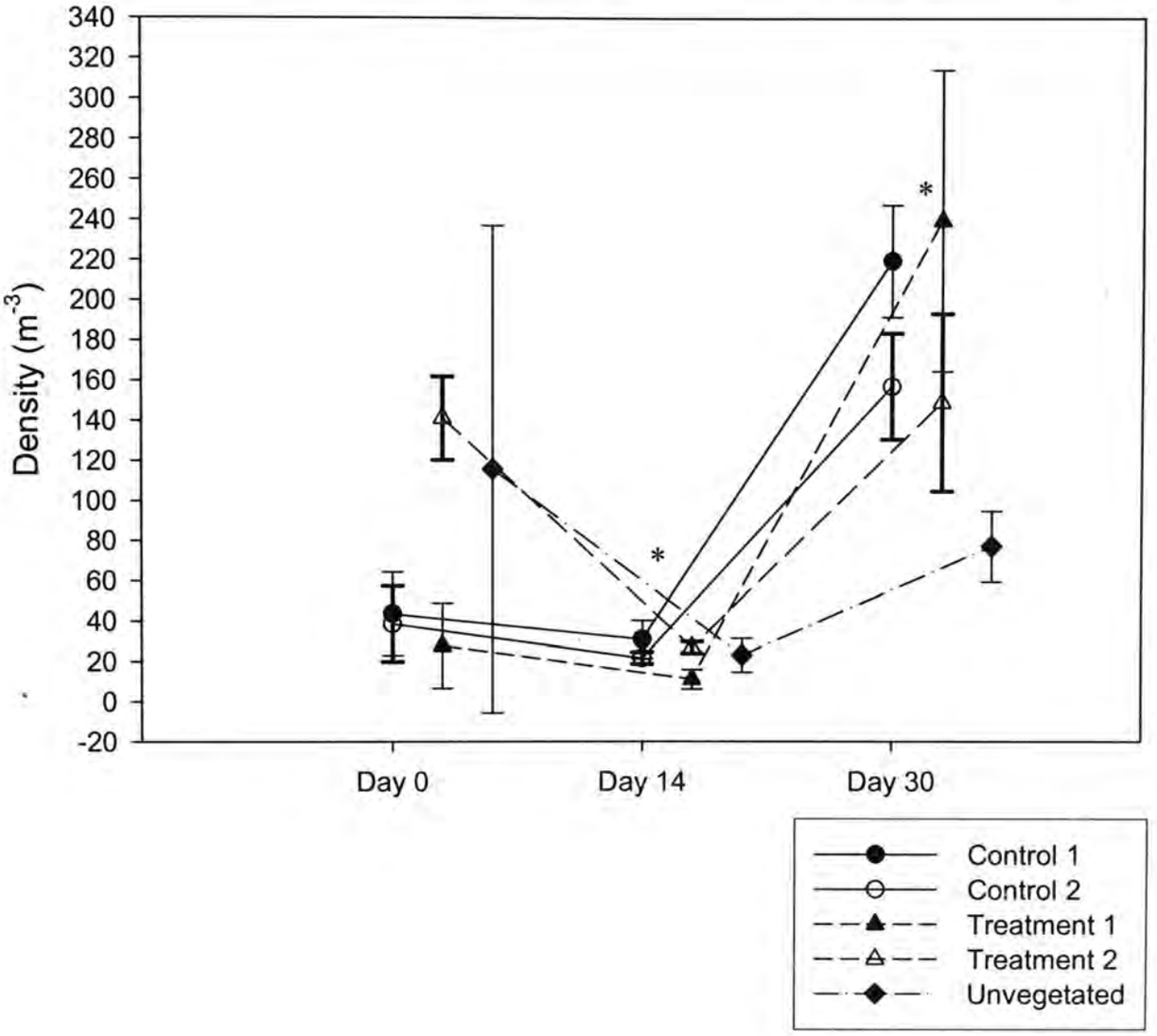


Fig. 3.3 Temporal change in mean (± S.D.) zooplankton density in control, treatment and unvegetated habitats. One-way ANOVA or Kruskal Wallis test results indicate significant differences in mean zooplankton density among sampling dates in all habitat types except the unvegetated habitat. One-way ANOVA results (df = 14) indicate significant differences in mean zooplankton density among habitats on Day14 (p = 0.033) and Day30 (p = 0.007) (as marked by *) of the experiment. Tukey test results display 3 statistically distinct groups (a, ab and b) on Day 14: (a). T1; (ab). C2, T2 & unv; (b). C1, and on Day 30: (a). unv; (ab). C2 & T2; (b). C1 & T1.

Control: ANOVA, F= 15.426, df= 17, p<0.001
Treatment: ANOVA, F= 10.015, df= 17, p=0.002
Unvegetated: ANOVA, F= 3.144, df= 8, p=0.116

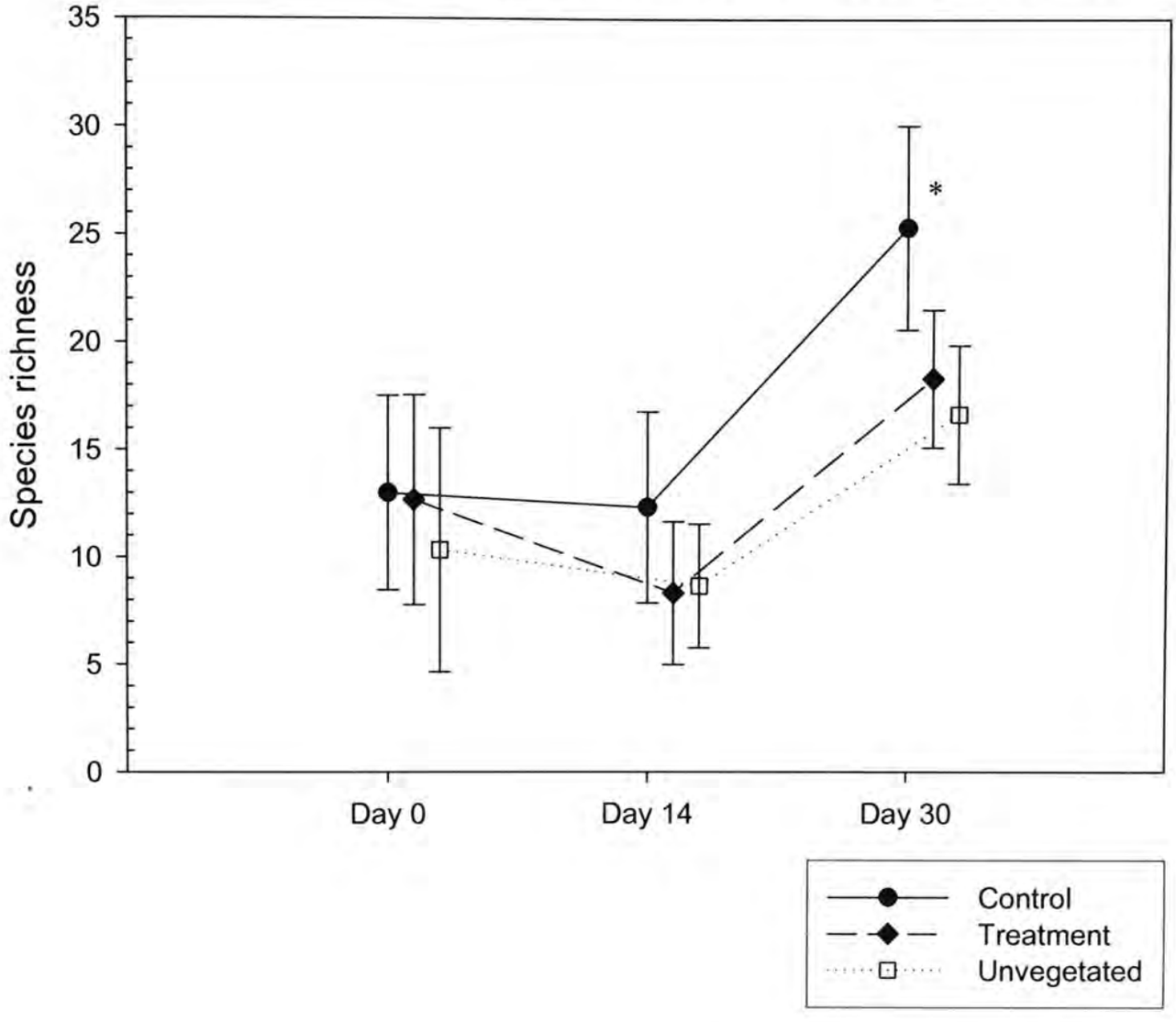


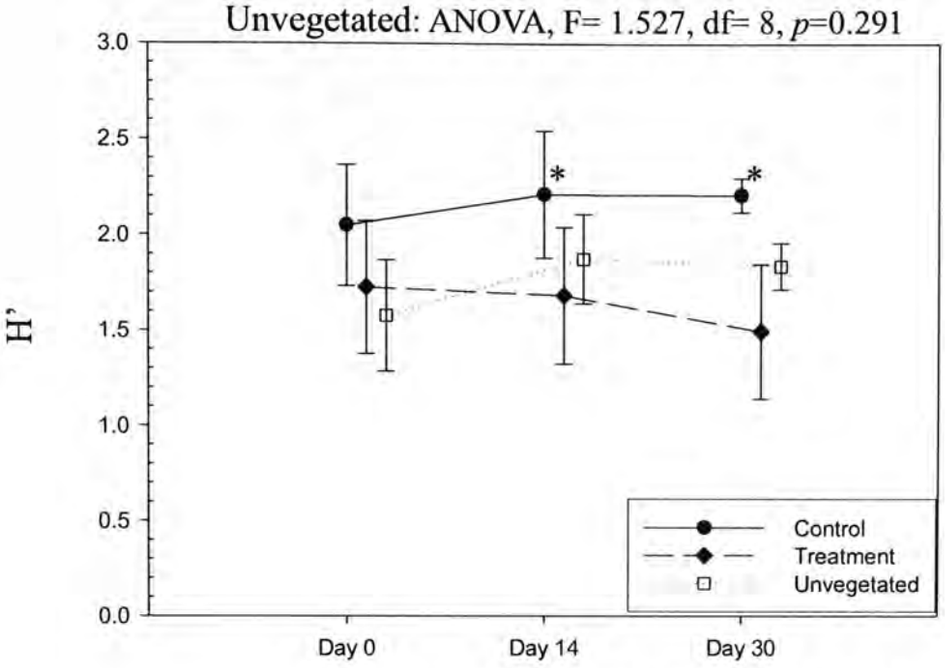
Fig. 3.4 Temporal change in mean (± S.D.) species richness in control, treatment and unvegetated habitats. One-way ANOVA results show significant differences in mean species richness among sampling dates in control and treatment samples but not in those from unvegetated habitat. The replicate data sets of each control or treatment sample were pooled as no significant differences in species richness were found between replicates of each habitat type. One-way ANOVA result (df = 14, p= 0.010) indicates significant difference in mean species richness among habitats on Day30 (as marked by *) of the experiment. Tukey test results display 2 statistically distinct groups (a and b) on Day 30: (a). treatment & unvegetated; (b). control.

Temporal change in H'

Control: ANOVA, F= 0.709, df= 17, p=0.508

Treatment: ANOVA, F= 0.727, df= 17, p=0.500

Unvegetated: ANOVA, F= 1.527, df= 8, p=0.291



Temporal change in J

Control: Chi-square= 14.749, df= 2, p=0.001

Treatment: ANOVA, F= 12.487, df= 17, p=0.001

Unvegetated: Chi-square= 4.356, df= 2, p=0.113

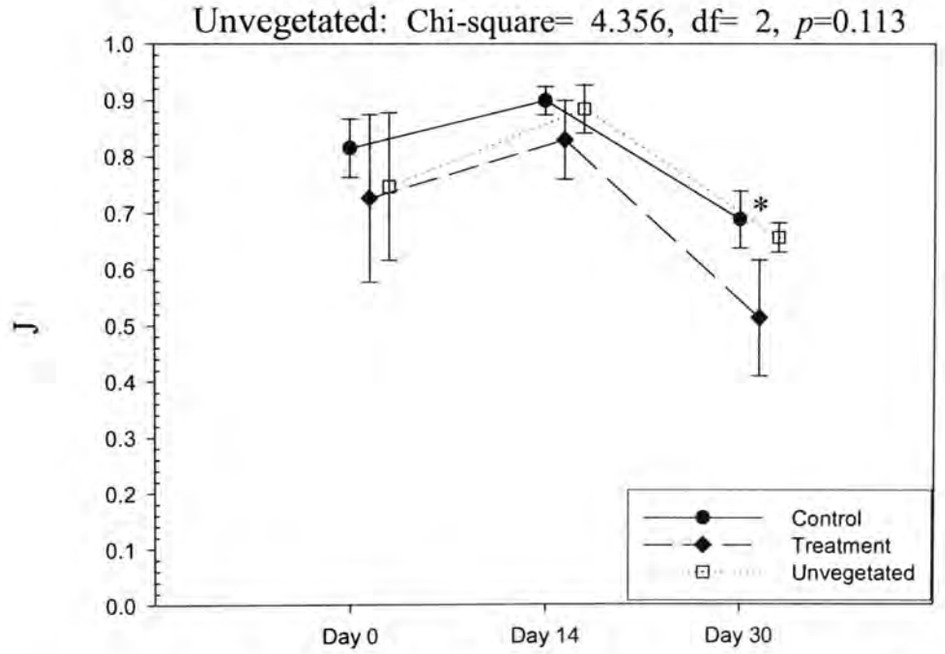


Fig. 3.5 Temporal change in mean (± S.D.) Shannon Diversity (H') and Evenness (J) Indices in control, treatment and unvegetated habitats. One-way ANOVA or Kruskal Wallis test results indicate significant temporal differences in J in both control and treatment habitats; significant among-habitat difference in H' on Day14 (ANOVA: df = 14, p = 0.049) and Day 30 (Kruskal-Wallis: df = 2, p = 0.004) and significant among-habitat difference in J on Day30 (Kruskal-Wallis: df = 2, p = 0.016) (as marked by *) of the experiment.

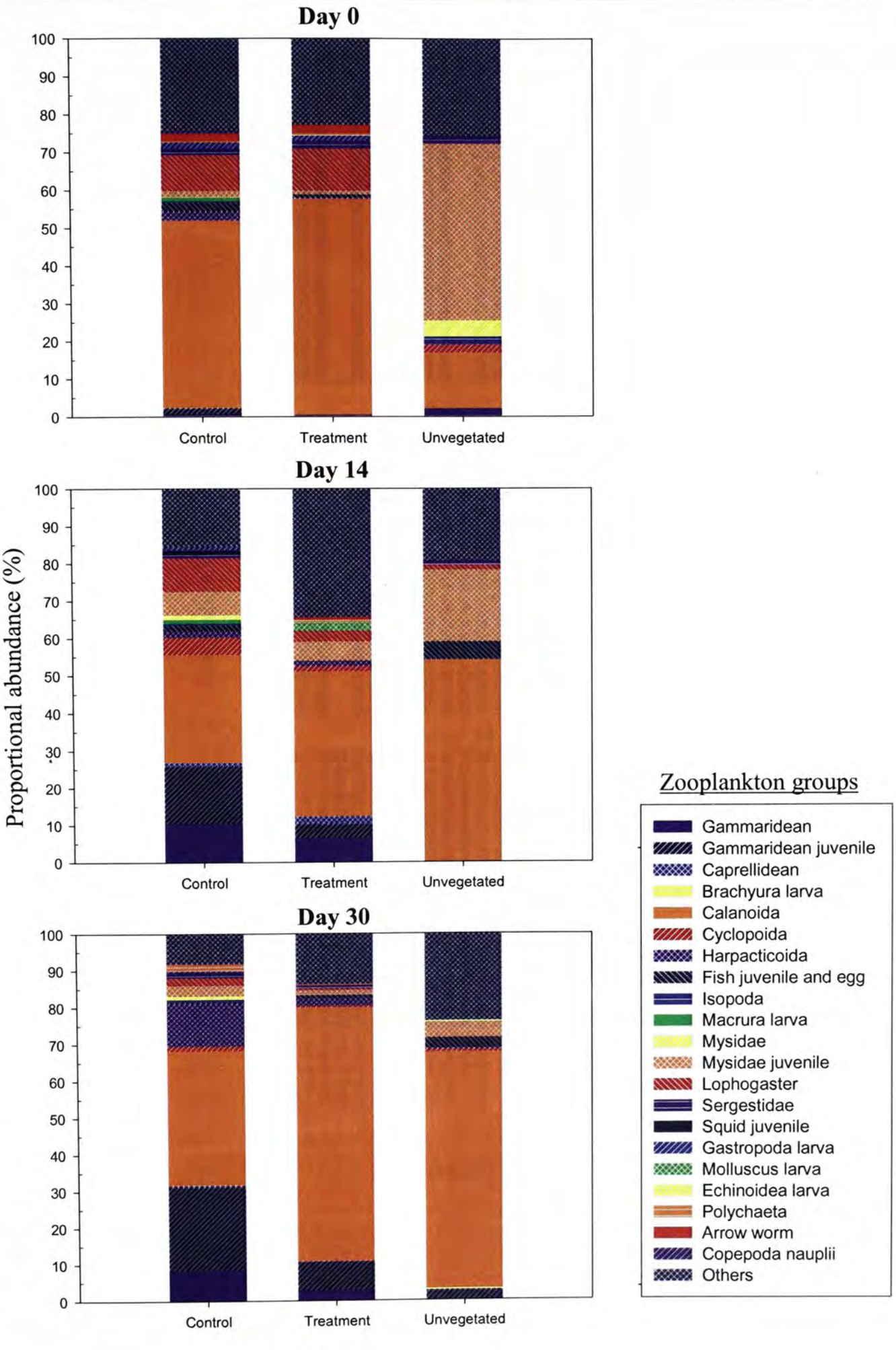


Fig. 3.6 Proportional abundance of zooplankton groups in control, treatment and unvegetated habitats on Days 0, 14 and 30 of the experiment.

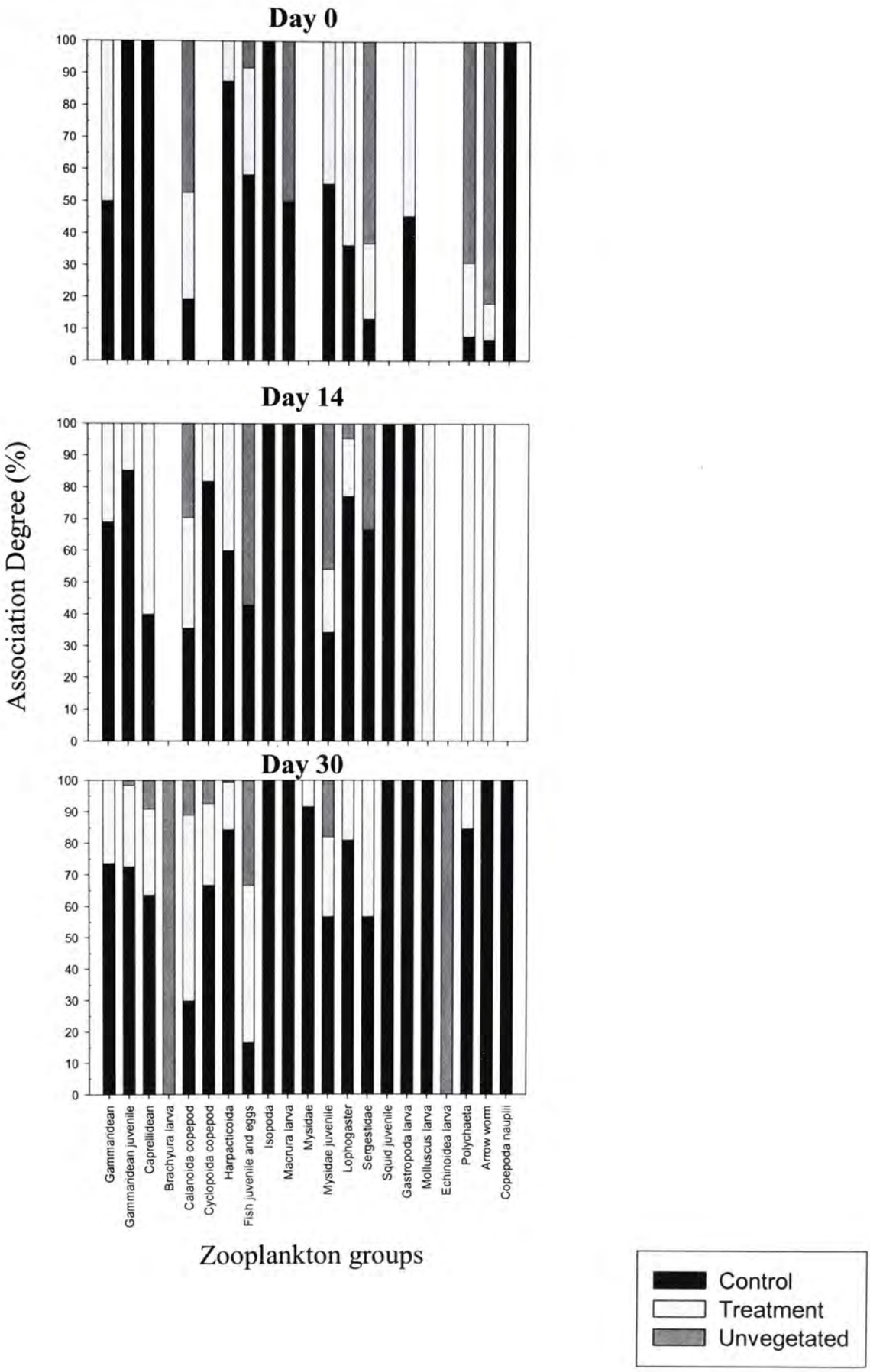


Fig. 3.7 Association degree of common zooplankton groups in control, treatment and unvegetated habitats on Days 0, 14 and 30 of the experiment.

Chapter 4

Epiphytic Faunal Assemblages in Seaweed Bed of *Sargassum siliquastrum* and Its Temporal Variation

4.1 Introduction

Macroalgal community is one of the highly productive ecosystems in the natural environment, with maximum productivity at 1.8 kg C m^{-2} yr^{-1}. Thus, macroalgae are essential primary producers. Macroalgae and their phytodetritus, together with the epiphytic algae, serve as a stable source of food for herbivores and periphyton consumers, and therefore for predators of these animals (Lubchenco 1978, Norton and Benson 1983, Peterson *et al.* 1984, Lüning 1990, Steneck and Dethier 1994, Raffaelli and Hawkins 1996, Steneck 1997, Bologna and Heck Jr. 1999, Lee *et al.* 2001, Chavanich and Harris 2002, Epifanio *et al.* 2003). Macroalgal detritus is also a significant source of nutrient for coastal marine ecosystems through the microbial food webs (Hicks 1980, Moreno and Jara 1984, Duggins *et al.* 1989). Pelgaic *Sargassum* species have been shown to release large amounts of dissolved organic material (Hansen 1977, Coston-Clements *et al.* 1991). Additionally, the concentration

of nitrates and phosphates in the water surrounding a floating *Sargassum* clump may be as much as 2 to 3 times the concentration outside the clumps in open water (Culliney 1970, Carpenter and Cox 1974, Phlips and Zeman 1990). The result is an environment of relatively enriched organic productivity for autotrophs as well as consumers. In addition as a source of organic food and nutrients in the open ocean, macroalgae (seaweeds) are able to provide refuge for the animals, like invertebrates, zooplankton, larvae and many others, to stay away from predation (Mathieson *et al.* 1976, Menge 1978, Heck and Thoman 1981, Edgar 1983c, Heck and Wilson 1987, Summerson and Peterson 1984, Hacker and Steneck 1990, Holmlund *et al.* 1990, Brawley 1992, Gagnon *et al.* 2003, Sapper and Murray 2003). Complex microhabitats were formed as a result of the presence of different plant parts (Leber 1985, Gotceitas and Colgan 1989, Jenkins and Sutherland 1997, Boström and Bonsdorff 2000, Hovel and Lipcius 2001). Gagnon *et al.* (2003) illustrated that the kelp canopy in shallow water, and movement of the kelp blades by waves, provided blue mussels *Mytilus edulis* with a spatial refuge from sea star predation by hindering the movement of the sea star *Asterias vulgaris* towards its prey. Macroalgal beds can ameliorate stress conditions, such as strong wave actions, by dampening the hydrodynamics around the beds and thus enhance sediment deposition (Orth 1977, Nicotri 1980, Gunnill 1983, Jackson 1985, Eckman *et al.* 1989, Johnson and Koehl

1994, Duggins and Eckman 1997, Pakhomov *et al.* 2002). This encourages larval settlement and recruitment within the bed, particularly around the vegetative canopy (Ekman 1983, 1987, Eckman and Duggins 1991, Irlandi and Peterson 1991, Harvey *et al.* 1995, Jenkins and Sutherland 1997, Rooker and Holt 1997, Boström and Bonsdorff 2000). As water velocity decreases, larvae can passively descend into the bed, allowing either passive or active selection of microsites within the vegetation. Furthermore, as larvae settle initially at the edge of the bed, the supply of larvae toward the centre or inner edge of the bed is reduced, creating a 'settlement shadow' (Roughgarden *et al.* 1988).

Worldwide, comparatively more explicit investigations have been carried out on faunal associates of pelagic *Sargassum* communities (Conover and Sieburth 1964, Fine 1970, Carpenter and Cox 1974, Ryland 1974, Bortone *et al.* 1977, Stoner and Greening 1984, Coston-Clements *et al.* 1991, Stachowicz and Lindquist 1997, Ólafsson *et al.* 2001) but less on the benthic *Sargassum* counterparts in the subtidal environment. Pelagic *Sargassum* clumps supported a diverse community of marine organisms including micro- and macro-fauna (Carpenter and Cox 1974), fungi (Kohlmeyer 1971), more than 100 species of invertebrates (Dooley 1972, Morgan *et al.* 1985), over 100 species of fishes (Dooley 1972, Bortone *et al.* 1977, Safran and

Omori 1990, Kingsford 1992, Yeh 1992), four species of sea turtles (Carr 1987, Manzella and Williams 1991), and marine mammals such as dolphins (Dooley 1972) in the Pacific and Atlantic Oceans. Dooley (1972) and Morgan *et al.* (1985) discovered the presence of copepods, decapod crustaceans, namely crab, shrimp and mysids, and their larvae, in addition to the commonly encountered barnacles, polychaetes, gastropods and bivalves in the pelagic *Sargassum* community. Stoner and Greening (1984) identified 1788 macrofaunal individuals in six phyla and 23 species in 78 individual floating clumps of *Sargassum fluitans* and *Sargassum natans* at the Gulf Stream and Sargasso Sea in the western North Atlantic Ocean. Carpenter and Cox (1974), Hansen (1977) and Coston-Clements *et al.* (1991) all reported nearly 60% of the total primary production in the upper 1 m water column in the western North Atlantic to be supported by the pelagic *Sargassum*. The downwell of the pelagic *Sargassum* would additionally provide a resource and nourishment for bottom dwelling consumers in the deep sea (Schoener and Rowe 1970).

The subtidal brown seaweeds have been studied as habitat for epiphytic fauna extensively along the Atlantic and Pacific Oceans (Edgar 1983b, Taylor and Cole 1994, Russo, A.R., 1997, Taylor 1998a, 1998b, Albertoni *et al.* 2001, Lippert *et al.* 2001, Christie *et al.* 2003, Leite and Turra 2003). In northeastern New Zealand, a

total of 73 epiphytic faunal taxa were found associated with 10 species of subtidal brown seaweeds (Taylor and Cole 1994). A total of 104 invertebrate species were identified to reside in six abundant macroalgal species in the Kongsfjord of the Arctic (Lippert *et al.* 2001). Over 175,000 animals belonging to 241 species were collected in five abundant species of macroalgae including *Sargassum* spp. at Tasmania (Edgar 1983b). In general, amphipods, isopods, copepods, polychaetes, shrimps, crabs, gastropods, bivalves, sea urchins and fish frequently utilize the subtidal seaweed beds as habitat, with the gammaridean amphipods and isopods representing the most abundant taxa (Edgar 1983a, 1983b, Taylor and Cole 1994, Russo 1997, Lippert *et al.* 2001). The gammarideans are food for pelagic as well as benthic fish and shrimps, e.g. *Corophium* spp., and have been used as seahorse feed in aquaculture in China. Due to massive feeding, schooling of fish was found to be associated with the presence of amphipods. High abundance of amphipods can thus be used to locate possible school of fish, and assist in commercial fishing (Chen 1980, Ren 2006). Macroalgal communities can therefore play vital roles in marine ecosystems as habitats for ecological and even economically important fishery resources. However, despite its being a highly productive ecosystem, macroalgae bed as habitat for marine fauna and flora has been largely understudied and its essential role underappreciated in the Western Pacific along the coast of China, not to mention in Hong Kong where

Sargassum spp. are commonly found and can exist as extensive bed during their rapid growth and reproductive stages.

Phytal communities are structured by a variety of physical and chemical factors which include algal shape (Hicks 1977, Edgar 1983a, Taylor and Cole 1994, Ingólfsson 1995, Lippert *et al.* 2001), water depth (Edgar 1983a), wave exposure and water movement (Norton 1971, Fenwick 1976), season (Conover and Sieburth 1964, Fine 1970, Mukai 1971, Ryland 1974, Norton and Benson 1983, Stoner and Greening 1984), turbidity and detrital load (Moore 1974, Edwards 1980), and eutrophication as a consequence of pollution (Jones 1973, Albertoni *et al.* 2001). Temporal changes in faunal abundance associated with macroalgae have mainly been attributed to the seasonal epiphytic algal bloom coinciding with the peak growth of the macroalgae (Hagerman 1966, Mukai 1971, Cattaneo 1983, Edgar 1983b, Edgar 1990, Taylor 1998a, Albertoni *et al.* 2001) or to the seasonal abundance of the host alga itself that fluctuated with its growth pattern (Paine and Vadas 1969, Himmelman and Carefoot 1975, Steele and Whittick 1991). The faunal assemblage associated with the brown seaweed *Sargassum muticum* was found to vary temporally with its phenology (Norton and Benson 1983). Moreover, the seasonality of the motile associates of pelagic *Sargassum* spp. was probably confounded by variation related

to the ages of individual algal clumps, resulting in different epibiotic composition and abundance which in turn affected food supply of the motile invertebrates (Conover and Sieburth 1964, Fine 1970, Ryland 1974, Stoner and Greening 1984). In general, seasonality of faunal assemblage structure was a consequence of seasonal supply of macroalgae and their epiphytes as food, which fluctuated with the phenology of the host seaweeds. The two-way interaction between macroalgae and their resident herbivores has been highlighted. Grazing by crustaceans and marine mammals can reduce macroalgal biomass which in turn negatively affects the associated faunal community (Tegner and Dayton 1987, Duffy 1990, Geertz-Hansen *et al.* 1993, Trowbridge 1993, Sfriso and Pavoni 1994, Nakaoka 2005). On the other hand, grazing by these animals can cast a positive effect on their host macroalgal growth (Brawley and Adey 1981, D'Antonio 1985, Dudley 1992, Jernakoff and Nielson 1996, Kamermans *et al.* 2002). Kamermans *et al.* (2002) reported a beneficial impact of herbivorous amphipod *Gammarus locusta* and isopod *Sphaeroma hookeri* on *Ulva* spp.. Growth was probably brought about by their preferential removal of epiphytic diatoms from the algal thalli that increased the amount of light received by their host alga *Ulva* spp. Foraging by herbivorous amphipods on epiphytes of red alga *Rhodomela larix* increased the growth rate of the host alga and its reproductive output, suggesting an advantageous effect on the host

plant (D'Antonio 1985).

Apart from seasonality in food provision, macroalgal structural complexity has been considered to be one of the factors regulating the associated faunal assemblage structure in terms of abundance and species diversity throughout a year (Hicks 1977, Stoner 1979, 1982, Edgar 1983a, Russo 1987, Hacker and Steneck 1990, Taylor and Cole 1994, Aikins and Kikuchi 2001, Lippert *et al.* 2001, Danovaro and Fraschetti 2002, Schmidt and Scheibling 2007) or along the algal succession stages (Dean and Connell 1987a, 1987b). Enhanced structural complexity could give rise to reduced foraging efficiency of predators on fauna associated with the algae (Stoner 1972, 1982, Pfister and Hay 1988, Gagnon *et al.* 2003, Poore and Hill 2005). Biomass of the macroalgae has been known to impose a direct positive influence on the density of the associated macrofauna (Mukai 1971, Stoner 1980, Stoner and Lewis 1985, Russo 1989, Aikins and Kikuchi 2001, Albertoni *et al.* 2001, Leite and Turra 2003, Kraufvelin *et al.* 2006) as well as its species richness (Stoner and Greening 1984, Stoner and Lewis 1985).

Composition of epiphytic faunal assemblage associated with the brown algal bed of *Sargassum siliquastrum* and its temporal variation was illustrated in the present

Chapter. On the other hand, relationships between faunal assemblage and the structural complexity of the host alga have also been investigated and are discussed in more details in Chapter 5.

4.2 Materials and Methods

4.2.1 Sample collection

Epiphytic faunal samples on *Sargassum siliquastrum* were collected in three sites: Lung Lun Tsui (LLT), Lung Lok Shui (LLS) and Lo Fu Ngam (LFN). In each site, at least 18 *Sargassum siliquastrum* plants of different sizes were obtained haphazardly using labeled bags of 125 μm mesh size during the rapid growth, reproductive and dieback stages of *Sargassum siliquastrum* (i.e. from September to February). At least 10 replicate plants of different sizes were collected in the same way at the time of slow growth (i.e. from March to August). The whole plant was enclosed by the mesh bag gently, and the plant removed from its base, including the holdfast, and carried back to the laboratory. The whole course of sampling was performed from November 2006 to February 2008. Due to bad weather conditions and logistic problems, no samples were collected in some months: Apr07, Jul07 and Jan08 at LLT; Mar07,

Jul07, Aug07, Sep07 and Jan08 at LLS; May07 at LFN. For easy reference, samples collected during the rapid growth stage (i.e. from September to November) in the year 2006 were denoted as '06 Rapid growth' and those in the year 2007 as '07 Rapid growth', and so on.

During the sampling period, the sea surface temperature, salinity and dissolved oxygen level were recorded, using a portable multi-meter (Model 85, YSI Inc., USA) on the same date of sample collection.

4.2.2 Data acquisition

In the laboratory, *Sargassum siliquastrum* plants were initially immersed in a bucket containing 6L freshwater with 10ml formalin for 2 minutes to stun the epiphytic fauna, followed by vigorous washing for 2 minutes. Washing was carried out twice for each plant. Detached fauna were then sieved through a 500μm mesh sieve. The sampling bags and buckets were also rinsed using freshwater with formalin and then sieved through the 500μm mesh sieve to collect any remaining fauna. The epiphytic fauna obtained were fixed in 70% alcohol immediately after sieving and stored in labeled 250mL vial bottle. All animals were identified to the lowest possible taxon

level (e.g. family to species level) and counted using a dissecting microscope. Identification of fauna was verified with reference to Huang (2001). Length, fresh weight and number of branches (up to tertiary level) of each plant were determined after all epiphytic faunas were removed.

Epiphytic faunal density was expressed as number of individuals per 100g of algal wet weight. Species richness in this study referred to number of species and faunal taxon groups. Diversity was calculated and expressed as species richness and Shannon Diversity Index H' (Margalef 1958, Pielou 1966, 1975, Hurlbert 1971) or Evenness Index J (Margalef 1958, Pielou 1966, Hurlbert 1971). Averages of density, species richness, Shannon diversity Index H' and Evenness Index J were reported with standard deviation. The proportional abundance of the common epiphytic faunal groups collected from each sampling month was compared by calculating percentage of individuals belonging to the same taxonomic group over total number of individuals.

4.2.3 Data analysis

From November 2006 to February 2008, 102 *Sargassum siliquastrum* plants were

sampled at LLT, 86 at LLS and 117 at LFN. Therefore, a total of 305 *Sargassum siliquastrum* plants were collected in the three study sites. All statistical analyses were performed using SPSS 13.0 for Windows (SPSS Inc., USA). All data were tested for normality by Kolmogorov-Smirnov test or homogeneity of variance by Levene Median test. Transformation of the data was carried out if the parametric assumptions were not met. Non-parametric analyses were used instead if transformations of data still failed to satisfy the assumptions of the parametric tests. The significance level (p value) of all statistical analyses was set at 0.05.

To detect the temporal change and among-site difference in epiphytic faunal density, species richness, Shannon diversity Index H' and Evenness Index J, either parametric one-way ANOVA or non-parametric Kruskal-Wallis test was performed. In addition, to evaluate the temporal variation in density of the common groups, non-parametric Kruskal-Wallis test was carried out. Relationships between epiphytic faunal assemblage, in terms of density and Shannon diversity Index H', and environmental parameters, namely temperature, salinity and dissolved oxygen, were evaluated using regression analyses. Generalization of results was based on the interpretation from two out of the three study sites.

Epiphytic faunal community structures in terms of abundance and species composition were subjected to non-metric multidimensional scaling ordination (MDS) and cluster analysis using the Bray-Curtis similarity measure with 1000 times of permutation by SIMPROF. Two-dimensional MDS plots were mostly displayed in this study, but 3-dimensional MDS plots were shown instead if stress value of the corresponding 2-dimensional plots was larger than 0.20. ANalysis Of SIMilarities (ANOSIM), and sometimes additional Pairwise ANOSIM was employed to test the statistic for significant differences ($p<0.05$) between groups and SIMilarity of PERcentages (SIMPER), to identify the discriminating taxa between groups. Standardization and fourth-root transformation were performed on the abundance data prior to the analyses. All community analyses were done using PRIMER 6 software (Clarke and Warwick 2001).

4.3 Results

4.3.1 Temporal Change in Epiphytic Faunal Assemblage Composition and Comparison among Sites

Through the whole course of sampling, a total of 163 species (including

morpho-species) and taxonomic groups of epiphytic organisms on *Sargassum* were identified in the three sites LLT, LLS and LFN. Of these 163 species and groups recorded, 140 were encountered in LLT (Table 4.1), 141 in LLS (Table 4.2) and 133 in LFN (Table 4.3). In these three sites, no distinct groupings of epiphytic faunal assemblages among sampling months were detected based on the MDS plots (Figures 4.1A, 4.2A and 4.3A), implying that there was only weak variation in the faunal community structure over time. This pattern was further supported by the cluster dendrograms (Figures 4.1B, 4.2B and 4.3B). At a similarity level of about 35%, five main clusters of samples were formed at LLT (Figure 4.1B). These clusters consisted of: (1) Jun-Oct07; (2) Jun-Aug07; (3) Nov06 and Jun07; (4) Dec06, Jan-Feb07 and Sep07-Feb08; and (5) Nov06 samples. Four of these clusters, (1); (2) & (3); (4); and (5) were statistically distinct.

At LLS, 10 prime clusters were obtained at a similarity level of around 35% (Figure 4.2B), including samples in: (1) Dec06 and Jan07; (2) Nov06; (3) Jun07; (4) Nov06, Oct07 and Nov07; (5) Nov06 and Jun07; (6) Nov06, Jan07, Feb07, Oct07 and Nov07; (7) Jan07, May07, Dec07 and Feb08; (8) Nov06, Jan07 and May07; (9) Oct07-Feb08; and (10) Jan-Feb07. Except for (2) & (3), nine of the other clusters were statistically significantly different from one another.

At LFN, at a similarity level of about 35%, seven major clusters of samples were detected (Figure 4.3B), consisting of: (1) Mar07-Apr07 and Dec07-Feb08; (2) Jun07, Sep07 and Nov07; (3) Nov06, Aug07 and Nov07; (4) Dec06 and Jun07; (5) Nov06, Feb07, Jun07 and Oct07; (6) Dec06, Jun07, Aug07, Sep07 and Nov07; and (7) Jul07 and Aug07 samples. Among these clusters, four main statistically significant groups were revealed: (1); (2); (3), (4) & (5) and (6) & (7).

Significant differences in faunal assemblage between each sampling month were further revealed by ANOSIM, the details of these differences are given in Table 4.4A for LLT, Table 4.5A for LLS and Table 4.6A for LFN. In general, the main differentiating taxa among months at LLT included the gastropod larvae, harpacticoids, brittle stars, caprellideans and gammaridean juveniles. Similarly, gammaridean juveniles, caprellideans and harpacticoids were the principal discriminating taxa at LLS and LFN.

With respect to the growth stages of *Sargassum siliquastrum* in the three study sites, no distinct groupings of epiphytic faunal assemblages were revealed by the MDS plots (Figures 4.4A, 4.5A and 4.6A), inferring no apparent differences in faunal assemblages among seaweed growth stages. In addition, cluster dendrograms

(Figures 4.4B, 4.5B and 4.6B) showed that at LLT, eight major clusters of samples were formed at a similarity level of about 40% (Figure 4.4B). Each group was mainly comprised of samples from seaweed stages of: (1) 06 and 07 Rapid growth; (2) 07 Slow growth; (3) 07 Slow growth; (4) 06 Rapid growth, 07 Slow growth and 07 Rapid growth; (5) 07 Rapid growth and 07 Reproductive; (6) 07 Rapid growth, 07 Reproductive and 08 Dieback; (7) 06 Reproductive, 07 Dieback, 07 Slow growth and 07 Reproductive; (8) 06 Rapid growth. Among these eight clusters, six statistically significant groups were found: (1) & (2); (3) & (4); (5); (6); (7); and (8).

At a similarity level of around 35%, nine main clusters of samples were observed at LLS (Figure 4.5B). Each group primarily consisted of samples from seaweed stages of: (1) 06 Reproductive; (2) 06 Rapid growth; (3) 07 Slow growth; (4) 06 Rapid growth, 07 Slow growth and 07 Rapid growth; (5) 06 and 07 Rapid growth; (6) 06 Reproductive, 07 Slow growth, 07 Reproductive and 08 Dieback; (7) 06 Rapid growth, 06 Reproductive, 07 Dieback, 07 Slow growth and 07 Rapid growth; (8) 07 Rapid growth, 07 Reproductive and 08 Dieback; and (9) 06 Reproductive. Among these nine clusters, eight of them were statistically significant groups except for (2) & (3) which formed one single group. At LFN, eight major clusters of samples were obtained at a similarity level of about 35% (Figure 4.6B). Each group mainly

contained samples from seaweed stages of: (1) 06 Reproductive; (2) 06 Rapid growth, 06 Reproductive and 07 Dieback; (3) 07 Slow growth and 07 Rapid growth; (4) 06 Rapid growth, 07 Slow growth and 07 Rapid growth; (5) 06 Reproductive and 07 Slow growth; (6) 06 Rapid growth, 06 Reproductive, 07 Dieback, 07 Slow growth and 07 Rapid growth; (7) 07 Slow growth and 07 Rapid growth; and (8) 07 Slow growth. Among these eight clusters, five principal statistically significant groups were formed, consisting of: (1); (2); (3); (4), (5) & (6) and (7) & (8).

On the whole, results of the cluster analyses displayed a considerably more distinct grouping of samples from rapid growth, reproductive and dieback stages of *Sargassum siliquastrum* while samples from slow growth stage tended to merge with those from other stages or otherwise, stayed as outlier among samples in the three sites. Results of pairwise ANOSIM analyses (Tables 4.4B, 4.5B and 4.6B) further revealed the significant differences in faunal assemblages between each growth stage at a finer scale for each site. SIMPER analyses showed the important discriminating taxa between seaweed growth stages. In general, gastropod larvae and harpacticoids contributed most significantly to the differences in the faunal assemblages among growth stages at LLT (Table 4.4B); whereas gammaridean juveniles were important for LLS (Table 4.5B); and gammaridean juveniles, caprellideans, barnacles as well as

harpacticoids for LFN (Table 4.6B).

Although temporal differences in epiphytic faunal assemblage among sampling months as well as among seaweed growth stages were not very distinct, inter-annual disparity in epiphytic faunal assemblage structure could still be illustrated based on both sampling months and seaweed growth stages in the three study sites (Figures 4.7, 4.8 and 4.9). Based on MDS ordination, these assemblages did not shift back to their original position in the plot depicting the corresponding sampling period or growth stages over time, suggesting modifications had occurred in their structures over this period.

Throughout the sampling period, significant among-site difference with considerable overlapping in epiphytic faunal assemblage was detected in which faunal assemblage at LFN was distinctly different from those at LLT and LLS (Figure 4.10). The latter two shared substantial similarity in their faunal assemblages. Based on SIMPER analysis, gammaridean juvenile was the prime discriminating taxon among sites. With respect to each *Sargassum siliquastrum* growth stage, significant differences in faunal assemblage among sites were detected only during 06 Rapid growth and 08 Dieback stages (Figure 4.11).

4.3.1.1 Temporal Change in Epiphytic Faunal Density and Comparison among Sites

Throughout the sampling period, 1167 individuals per 100g seaweed were encountered at LLT (Table 4.1), 871 were counted at LLS (Table 4.2) and 1210 were found at LFN (Table 4.3). Differences in epiphytic faunal density among sites were statistically significant (Kruskal-Wallis test, Chi-square= 24.803, df=2, $p<0.05$).

At LLT (Figure 4.12A), the mean (± S.D.) faunal density remained relatively constant at about 30 individuals per 100g seaweed from Nov06 to Mar07 and reached its peak at 187.43 ± 68.66 individuals per 100g seaweed in May07. The density dropped back to the previous low level of about 30 individuals per 100g seaweed from Jun07 on and the highest density at 638.72 ± 199.91 individuals per 100g was attained in Feb08. At LLS (Figure 4.12B), the value of mean faunal density fluctuated more extensively when compared with that observed in LLT and LFN but was within the range of 21.08 ± 16.12 in Jun07 to 191.91 ± 128.50 individuals per 100g seaweed in Dec07. At LFN (Figure 4.12C), the mean faunal density remained relatively steady at about 20 individuals per 100g seaweed from Nov06 to Feb07 and a drastic increase to a peak at 337.67 ± 70.50 individuals per 100g seaweed was spotted in Apr07. The density returned to a low level from Jun07 on while the

maximum density at 357.52 ± 183.43 individuals per 100g was attained in Feb08. Significant temporal variation in epiphytic faunal density (Kruskal-Wallis test: df=12 [LLT]; df=10 [LLS]; df=14 [LFN], $p<0.05$) was detected in all three sites.

4.3.1.2 Temporal Change in Epiphytic Faunal Species Richness and Comparison among Sites

Significant variation in mean species richness of the epiphytic fauna was observed over time in LLT (ANOVA: df=101, $p<0.05$) (Figure 4.13A). The annual pattern appeared to be consistent between years. The mean (± S.D.) species richness increased gradually from Nov06 and attained its maximum at 22.00 ± 4.90 in Feb07. A steady drop then followed and hit its lowest value at 6.83 ± 3.06 in Jun07. The value increased gradually again thereafter, attaining its second maximum at 21.44 ± 5.17 in Feb08. The mean (± S.D.)Shannon-Weiner diversity index (H') (Figure 4.14 A) varied significantly (ANOVA: df=101, $p<0.05$) in a similar manner but at a lesser extent than that in mean species richness. The maximum mean H' at 2.21 ± 0.28 was reached in Feb07. The minimum at 1.43 ± 0.45, however, was reached in Feb08 when the species richness was maximum. Mean (± S.D.) evenness (J) was relatively more stable, although the levels of temporal variation were also statistically

significant (Kruskal-Wallis test: df=12, $p<0.05$). Its values varied within the range from 0.48 ± 0.18 in Feb08 to 0.94 ± 0.05 in Aug07.

At LLS (Figure 4.13B), mean species richness stayed comparatively constant near 10 from Nov06 to Feb07, followed by alternate rise and fall thereafter before reaching its peak at 17.56 ± 6.25 in Dec07. Significant temporal difference in mean species richness was detected (ANOVA: df=85, $p<0.05$). The trend in mean Shannon-Weiner diversity index (H') (Figure 4.14 B) varied quite the opposite to that for mean species richness. Significant temporal difference in mean H' was detected (ANOVA: df=85, $p<0.05$) with the highest value at 2.46 ± 0.31 recorded in Oct07 and the lowest at 1.73 ± 0.44 in Dec07. Mean evenness (J) values were relatively constant within the range from 0.56 ± 0.14 in Dec07 to 0.94 ± 0.05 in Nov06. Nevertheless, this variation over time was statistically significant (Kruskal-Wallis test: df=10, $p<0.05$).

At LFN (Figure 4.13C), there was also significant variation in mean species richness over time (ANOVA: df=116, $p<0.05$). Mean species richness remained relatively constant from Nov06 to Feb07 but experienced a drastic increase since then, hitting its maximum at 21.20 ± 3.56 in Mar07. A dramatic drop followed but a significant second minimum at 5.83 ± 3.25 was attained in Aug07. Thereafter, the value

increased slightly and fell to its significant lowest point at 5.67 ± 2.24 in Nov07. A steady rise was then observed, reaching its second maximum at 16.78 ± 4.15 in Feb08. The temporal change in mean H' fluctuated in a pattern that is different from that observed in species richness (Figure 4.14 C). Significant temporal difference in mean H' was recorded (ANOVA: df=116, $p<0.05$). Mean H' stayed at a relatively high value above 1.5 throughout the sampling period and attained its maximum at 1.92 ± 0.44 in Jan07. A significant lowest value at 1.12 ± 0.35 was recorded in Aug07. Mean evenness index (J) varied analogously with H' but in a smaller magnitude across the sampling months. Its values fell within the range from 0.50 ± 0.08 in Mar07 to 0.94 ± 0.04 in Nov07, with significant temporal difference obtained (Kruskal-Wallis test: df=14, $p<0.05$).

A total of 163 species and taxonomic groups of epiphytic fauna were identified in the *Sargassum siliquastrum* beds in the three study sites, with 140 species or taxa encountered at LLT (Table 4.1); 141 at LLS (Table 4.2); and 133 at LFN (Table 4.3). Statistically significant among-site differences in mean species richness (ANOVA: F= 6.115, df= 304, $p<0.05$) and mean H' (ANOVA: F= 10.834, df= 304, $p<0.05$) were detected. Post-hoc test results suggest that species diversity in LLT and LLS was statistically similar and was different from that in LFN. In general, species

commonly encountered in LLT and LLS were not the same as those in LFN (Tables 4.1-4.3).

4.3.1.3 Temporal Change in Epiphytic Faunal Species Composition

Figure 4.15 illustrates the proportional abundance of common epiphytic faunal groups in the three sites. At LLT (Figure 4.15A), over the whole course of sampling, gammaridean juveniles were consistently the leading dominant group (accounting for about 10-75% of the total population), followed by the gammaridean amphipods (6-20%), the barnacles (3-40%), the gastropods (10-45%), the bivalves (1-6%), the isopods (1-10%), and the harpacticoid copepods (0.2-11%). Figure 4.16 shows the population dynamics of the common groups over the sampling period in LLT. Significant temporal variations in density were observed in population dynamics of the gammaridean juveniles, gammarideans, barnacles, gastropods and harpacticoids (Kruskal-Wallis test: df=12, $p<0.05$). Generally, these common groups were at their maximum abundance in Feb08, particularly the gammaridean juvenile, gammaridean, gastropods and harpacticoids. Additionally, barnacle reached its peak abundance in May07. Bivalves and isopods existed in greater numbers in May07, Aug07 and Feb08. Harpacticoid copepod experienced its bloom in Dec06-Feb07 and Feb08.

Throughout the sampling months at LLS (Figure 4.15B), gammaridean juveniles (made up around 3-70% of the total population) and gastropods (10-60%) were consistently the principal dominant groups, followed by the gammaridean amphipods (1-11%), the barnacle (0.4-29%), the bivalves (1-14%), the isopods (0.1-5%), and the hermit crab of infraorder Anomura (2-11%). Figure 4.17 shows the population dynamics of the common groups over the sampling time. The gammarideans and their juveniles, barnacles, gastropods and bivalves experienced significant temporal variations in density (Kruskal-Wallis test: df=10, $p<0.05$). Both gammarideans and their juveniles reached their highest abundances in Dec07 and Feb08. Barnacles and bivalves obtained their greatest number in Jan07. Gastropods and isopods were most numerous in Nov06 and Oct07. Peak density of hermit crabs was spotted in Apr07.

At LFN (Figure 4.15C), gammaridean juveniles (contributing about 1-57% of the total population), barnacles (4-47%) and gastropods (1-27%) were consistently the prevailing common taxa, followed by the gammaridean amphipods (1-12%), the bivalves (1-14%), the isopods (1-20%), the hermit crab of infraorder Anomura (1-7%) and the harpacticoids (3%). Figure 4.18 shows the population dynamics of the common groups in LFN. Significant differences in density with time were recorded in the population dynamics of gammaridean and their juveniles, barnacles,

gastropods, bivalves, isopods and harpacticoids (Kruskal-Wallis test: df=14, $p<0.05$). Gammaridean and their juveniles attained their highest abundances in Mar07, Apr07 and Feb08. Peak densities of barnacles and gastropods appeared in Apr07 while that of bivalves in Jun07. Maximum abundances of isopods and hermit crabs occurred in Apr07 and Jul07. Harpacticoids attained their highest density in Jan08.

Tables 4.1, 4.2 and 4.3 present the mean density of each species and taxonomic groups identified in the three sites over the sampling months. For the gammaridean amphipod, family Talitridae included the species *Peramphithoe orientalis* among the four morpho-species and *Guernea* spp. among the two morpho-species of family Dexaminidae. Certain species or families consistently dominated in the three sites. Examples of these included the amphipod families Talitridae, Stenothoidae and Synopiidae; the gastropods *Pyrene scripta* and *Mitra* spp., with *Tectarius* spp. additionally being abundant in LFN; and the bivalves *Septifer viridis* and *Chama reflexa*. Some taxonomic groups, namely the Amphipoda, Gastropoda and Bivalvia, singularly appeared in high species diversity at certain times in all sites. In particular, high diversity of 10-12 species of amphipods was recorded generally in Mar07 and Feb08; 14-15 species of gastropods in Jan07-Mar07, Dec07 and Feb08 at LLT, 16-19 species in Jan07, Oct07 and Dec07 at LLS, and 12 species in Nov06 at LFN. Among

the Bivalvia, the highest diversity of 6 species appeared in Dec06 at LLT; 7-9 species in Nov06 to Jan07 at LLS; and 7-9 species in Oct07 to Feb08 at LFN. Specific timing of occurrence of some invertebrates, such as the gastropods, bivalves, brachyurans and stomatopods, as well as fish juveniles was also noted. The gastropod and *Lunella* spp. larvae appeared abundantly in Jan07 to Mar07, Dec07 and Feb08 at LLT; in May07 at LLS; and in Feb07 to Jul07 at LFN; while the adult *Lunella* spp. occurred in relative high abundance in late May07 at LLT. The Mytilid larvae (Bivalvia) generally showed up in Nov06, Dec06, Jan07 and Mar07 in the three study sites. For the brachyuran juveniles, the *Sargassum* crab juveniles appeared in Jan07 to Mar07 and May07, while the lobster juveniles in Feb07, Apr07, Oct07 and Feb 08 in all the sites. The stomatopod (i.e. mantis shrimp) juveniles appeared in Jan07 and Feb08 in LLT and LLS; while fish juveniles – *Sebastiscus marmoratus* could be found in Feb07, Jan08 and Feb08, the Blenniidae in Jan07, *Pelates quadrilineatus* of the family Terapontidae in Nov06 and Feb08, and *Petroscrites breviceps* of the family Blenniidae in Feb08. Certain species was found to carry eggs when discovered in the seaweed bed of *Sargassum siliquastrum* at specific time. The lophogaster *Lophogaster pacificus* was in high abundances especially in Dec06, Jan07, Jan08 and Feb08 in the three sites, with egg-bearing females to male ratio at approximately 3:1.

4.3.1.4 Occurrence of Caprellidean and its Variation with Seaweed Growth Stages

Significant temporal change in mean caprellidean density was detected in all sites (Kruskal-Wallis test: df=12 [LLT]; df=10 [LLS]; df=14 [LFN], $p<0.05$) (Figure 4.19). On the whole, caprellidean reached its maximum abundance in February, March and April. During Nov06 to Jun07, peak abundances of caprellidean were observed to appear right after the decrease in seaweed length in March 07. This phenomenon was singularly conspicuous at LFN. The bloom of caprellidean likely happened after the dieback of *Sargassum siliquastrum*.

4.3.2 Temporal Trends of Environmental Factors and their Relationship with Epiphytic Faunal Assemblage

Figure 4.20 shows the temporal trend of mean surface temperature, dissolved oxygen level and salinity in the three study sites. At LFN (Figure 4.20 A), the mean (± S.D.) water temperature initially dropped to a level of about 19 ℃ from Nov06 to Jan07. It remained relatively constant from Jan07 to Mar07 before starting to rise to the maximum at 30.47 ± 0.06 ℃ in Jul07. A gradual decline followed and the temperature reached its minimum at 13.43 ± 0.06 ℃ in Feb08. The dissolved oxygen

and salinity levels did not vary as large a magnitude as that observed for the temperature. The mean (± S.D.) dissolved oxygen level ranged from 4.15 ± 0.27 mg/L to 8.90 ± 0.28 mg/L. It stayed at a relative high value of over 6 mg/L from Dec06 to Mar07 and then diminished to a stable level at about 4 mg/L till Oct07, coinciding with the highest water temperatures recorded within the same period, before returning to a higher level after Nov07. The mean (± S.D.) salinity level remained comparatively constant around 32 ppt, except for a sudden plunge to 25.70 ± 0.44 ppt in Jun07. At LLT (Figure 4.20 B), the mean water temperature increased from 17.27 ± 0.06 ℃ to the maximum at 30.40 ± 0.00 ℃ in Jun07. A steady fall followed and reached its minimum at 13.73 ± 0.06 ℃ in Feb08. The mean dissolved oxygen and salinity levels did not change as much over time. The dissolved oxygen levels varied from 4.78 ± 0.06 mg/L in Oct07 to 7.17 ± 0.06 mg/L in Jan07. The salinity level remained relatively stable at about 32 ppt, except for a sudden drop to 24.60 ± 0.00 ppt in Jun07. At LLS (Figure 4.20 C), the mean (± S.D.) water temperature first diminished to a level of about 17 ℃ from Nov06 to Jan07 before a gradual raise to reach its maximum at 29.30 ± 0.00 ℃ in Jun07. A steady decline followed with the minimum at 14.13 ± 0.06 ℃ reached in Feb08. The mean (± S.D.) dissolved oxygen level remained relatively constant within the range from 4.77 ± 0.04 mg/L to 6.63 ± 0.16 mg/L. The mean (± S.D.) salinity level was also

comparatively stable around 33 ppt, except for a big drop to 24.37 ± 0.23 ppt in Jun07.

Both the mean faunal density and species diversity H' did not vary significantly with mean temperature (Figure 4.21), dissolved oxygen level (Figure 4.22) nor with the salinity levels (Figure 4.23). The epiphytic faunal density generally decreased while H' slightly increased with increase in temperature (Figure 4.21). On the other hand, faunal density increased whereas H' declined with increase in salinity (Figure 4.22). No general consistent trend between faunal assemblage structure and dissolved oxygen level was observed (Figure 4.23).

4.4 Discussion

4.4.1 Temporal Change in Epiphytic Faunal Assemblage Structure

In the main, no distinct groupings of epiphytic faunal assemblages among sampling months were detected based on the MDS ordination and cluster analyses. However, significant variation in faunal assemblage could be detected if grouped collectively between wet season (April-September) and dry season (October-March). Based on

the pairwise ANOSIM results, the gammaridean juveniles and caprellideans were the principal discriminating taxa between seasons in the three sites. These gammaridean juveniles were most numerous in February, March and April; while caprellidean attained its population bloom in February and March. Faunal assemblages during the rapid growth, reproductive and dieback stages of *Sargassum siliquastrum* were more similar when considered collectively and compared with that in slow growth stage. On the other hand, faunal community structure in seaweed reproductive stage displayed significant difference from that in the dieback stage with harpacticoid copepod being the principal discriminating taxon.

Peak abundance of epiphytic fauna was on the whole observed in late winter and early spring (Apr07, May07 and Feb08). This abundance was due mainly to the appearance of common faunal groups in tremendous number at that particular month. Collectively, peak abundance of total epiphytic fauna in Apr07 and May07 was a consequence of the occurrence of large number of gammarideans and their juveniles, barnacles, bivalves and isopods; whereas that in Feb08 was caused by the appearance of remarkably high number of gammarideans and their juveniles, harpacticoid copepods as well as gastropods, which coincided with the dieback stage of *Sargassum siliquastrum*.

The seasonal burst of food items might be one of the most pervasive factors affecting the abundance of epiphytic fauna associated with macroalgae (Edgar 1990). The flourish of periphyton on the green algae *Chara angolensis* favored the development of communities of the associated fauna with scraping and detritivore characteristics (Albertoni *et al.* 2001). Mukai (1971) found that smaller, truly phytal species of animals associated with winter growing *Sargassum* had peaks of abundance in winter that synchronized with the increase in algal standing crop. Albertoni *et al* (2001) found that the greatest biomass of gastropod *Heleobia australis* was attributable to the greater food availability provided by the periphyton of the aquatic macrophytes. The dominant taxa like gammaridean amphipods, molluscs and isopods included epiphytic algae in their diets (Hagerman 1966, Fauchald and Jumars 1979, Pavia *et al.* 1999, Kamermans *et al.* 2002). Some species of gammaridean amphipods consume primarily microalgae and detritus, while other species forage on macrophytes as well (Zimmerman *et al.* 1979, Brawley and Fei 1987, Hay *et al.* 1987, Duffy 1990). For example, gammarideans of the family Ampithoidae are herbivorous on macroalgae and are closely associated with seaweeds (Ren 2006). Most benthic gammaridean species and caprellidean amphipods are omnivores whose food items composed of algae, dead plant and animal detritus. For example, *Corophium* spp. are benthic amphipods living on seaweeds, hydras and sponges that forage upon organic detritus

(Ren 2006). Herbivorous amphipods or isopods used their macroalgal hosts both as food and habitat (Hay 1987, Poore 1994, Wahl and Hay 1995). This is true especially for the more sedentary herbivores, such as the amphipod *Ampithoe* spp. and *Cymadusa* spp., that consume selectively and live in close association with individual macroalgal hosts (Bernays and Graham 1988, Duffy and Hay 1994, Bernays and Minkenberg 1997, Cruz-Rivera and Hay 2000). Other than amphipods, a majority of gastropods, e.g. *Monodonta neritoides, Astraea rhodostoma, Cypraea gracilis*, *Tectus pyramis*, are grazers on algae; while some, e.g. *Oliva* spp., are scavenger on detritus (Hagerman 1966, Fauchald and Jumars 1979, Hill and Phillipps 1981, Orr 1985, Pavia *et al.* 1999, Kamermans *et al.* 2002). Harpacticoid copepods are detritivores foraging upon epiphytes and detritus (Hicks 1980, Coman *et al.* 2003). On the whole, herbivores were found to synchronize their life cycles to coincide with the seasonal bloom of higher-quality foliage (Van Soest 1994). Epiphytic algae were likely to respond to the same environmental conditions as macroalgae and consequently have similar phenologies (Conover 1964). *Sargassum muticum* was found to be heavily colonized by epiphytes in the British Isles shortly after the onset of fertility in summer (Jephson and Gray 1977). Therefore, it can be inferred that degree of epiphytization might be possibly higher at times of reproductive and dieback stages of *Sargassum siliquastrum* in the present study, supporting population blooming of

the abundant animal groups. Furthermore, temporal change in nutritious content of macroalgae could possibly regulate the associated faunal assemblage in terms of abundance and species richness. Significant seasonal variations in calorific content (i.e. total amount of stored chemical energy) of several marine algal species, such as the brown alga *Pilayella littoralis* in Newfoundland, was reported, with the suggestion that calorific content was correlated positively with reproductive activity (i.e. during reproductive stage) and inversely with maximal growth (i.e. during the rapid growth stage) (Paine and Vadas 1969, Himmelman and Carefoot 1975, Steele and Whittick 1991). The higher calorific value of the brown alga *Pilayella littoralis* was believed to support greater growth and reproductive rates of the intertidal amphipod *Gammarus lawrencianus* (Steele and Whittick 1991). During decomposition, the brown algae retained higher nutritional values and these values lost at a slower rate when compared with that in the red and green algae (Buchsbaum *et al.* 1991). The amphipod *Ampithoe longimana* fed heavily on brown macroalgae *Sargassum filipendula* over the red and green seaweeds (Duffy and Hay 2000). Feeding preferences and nutritional requirements, even among related species, can be dramatically different (Lubchenco 1978, Salemaa 1987, Duffy 1990, Duffy and Hay 1994, Pavia *et al.* 1999, Cruz-Rivera and Hay 2000, Sotka and Hay 2002, Sotka *et al.* 2003). The brown alga *Sargassum siliquastrum* in the present study could be

providing relatively higher nutritional values of plant tissue and phyto-detritus during its reproductive and dieback stages, when compared with the other growth stages. Thus faunal species can take advantage of the seasonal bloom of food source by synchronizing their life cycles (Johnson 1976, Heck and Wetstone 1977, Hicks 1980, Shafir and Field 1980, Taram and Wakabara 1981, Van Soest 1994). In particular, gammaridean amphipods generally have short generation times and can develop from newly produced juveniles to egg-bearing adults in a few weeks (Robertson and Lucas 1983, Hiwatari and Kajihara 1984, Duffy and Hay 1991, Graça *et al.* 1993, Kneib *et al.* 1997). They synchronize their reproduction, particularly in early spring (Che and Morton 1992, Ren 2006), to coincide with the reproductive and dieback stages of *Sargassum siliquastrum* in the current study. On the other hand, harpacticoid copepods are regarded as typical opportunists that undergo reproductive synchrony with rapid reproductive and generation turnover in times of favourable conditions, e.g. abundant food source (Hicks 1980). They were thus also abundantly found during the reproductive and dieback stages of *Sargassum siliquastrum* in the present study.

Variation in seaweed chemical defense with seaweed growth stage has been considered as one of the determinants in structuring the epiphytic faunal community.

Natural chemical compounds produced by algae, namely polyphenolic compounds and polar galactolipids, serve as a deterrent to herbivores (Paul 1987, Hay and Fenical 1988, Hay *et al.* 1987, 1988, Hay and Fenical 1988, Steinberg 1988, Hay 1996, Deal *et al.* 2003, Taylor *et al.* 2003, Pereira *et al.* 2004, Ceh *et al.* 2005, Amsler and Fairhead 2006, Paul *et al.* 2006, Wikström *et al.* 2006). They have even been shown to greatly reduce the feeding and survival of herbivores (Steinberg 1988, Schnitzler *et al.* 2001). In addition, chemical composition of marine algae varied seasonally (Paine and Vadas 1969). The increase in the quality of kelp species *Agarum fimbriatum* and *Alaria marginata* particles with age corresponded with a rapid loss of polyphenolic secondary metabolites and an increase in total nitrogen, hence promoting highest growth rates in both polychaete *Pseudochitonopoma occidentalis* and mussel *Mytilus trossulus* that depended on them (Duggins and Eckman 1997). This suggests that phytodetritus from the aged *Sargassum siliquastrum* at dieback stage in the present study might favor the foraging of detritivores, e.g. caprellidean and harpacticoid, when compared with those from younger plants in the other growth stages.

Secondary metabolites from marine algae commonly function as defenses against consumers and some, e.g. phorotannins from brown algae, act as anti-fouling, or

anti-microbial agents. Algae are able to produce allelochemical substances at or near the surface of the thallus which either directly ward off animals or prevent the growth of micro-epiphytes upon which epifaunas feed (Nicotri 1977, Steinberg 1984, D'Antonio 1985, Hay and Fenical 1988, De Nys *et al.* 1991, Schmitt *et al.* 1995, Clare 1996, Walters *et al.* 1996, Lau and Qian 1997, Dworjanyn *et al.* 1999, Steinberg and de Nys 2002, Nylund and Pavia 2003, Wikström and Pavia 2004, Amsler *et al.* 2005, Macaya *et al.* 2005, Amsler and Fairhead 2006). Only brown seaweeds produce polyphenolics, such as phlorotannins (Hay and Fenical 1988, Jennings and Steinberg 1994, Amsler and Fairhead 2006). Phlorotannins occurred in high concentrations, commonly 1-15% of dry mass, in many temperate brown seaweeds (Steinberg 1985, Ragan and Glombitza 1986, Estes and Steinberg 1988). Antifouling chemicals, namely brown algal phlorotannins, tannic acid and phloroglucinol, of macroalgae can inhibit larval settlement (De Nys *et al.* 1995, Walters *et al.* 1996, Lau and Qian 1997, Da Gama *et al.* 2002) and also impose negative impact on the post-settlement stages of fouling organisms (Schmitt *et al.* 1995, Da Gama *et al.* 2002, Wikström and Pavia 2004). Schmitt *et al.* (1995) noted that the surface of the brown alga *Dictyota menstrualis* contained terpene compounds that could lead to mortality, abnormal development, or reduced rates of development of the bryozoan *Bugula neritina* larvae. Thus larval settlement on the macroalgal

surface was prohibited when the larvae directly contacted the algal surface. Phlorotannins produced on the distal growing tips, i.e. younger branch tips, of *Sargassum* had an anti-fouling effect on colonizing epibionts (Conover and Sieburth 1964, Sieburth and Conover 1965). Antibiotic activity of marine algae in temperate regions has been shown to vary seasonally. The concentration of antifouling chemicals peaked in activity during algal active growth and dropped after reproductive stage (Sieburth and Conover 1965, Paine and Vadas 1969). It can thus be speculated that antifouling chemical content in *Sargassum siliquastrum* could likewise be lower after its reproductive stage. This explains the enhanced attachment of fouling organisms, namely barnacles and bivalves, during reproductive and dieback stages in the current study. This timing coincided with the recruitment period of these fouling faunas. The barnacles *Chthamalus* spp. were observed to undergo unimodal pattern of settlement in a single short period during wet season (Wu 1974) and most subtropical bivalve species in Hong Kong were recorded to undergo twice-a-year recruitment pattern in spring (February-March) and autumn (October-December) (Che and Morton 1992, Morton 1992, Chiu 1998).

Apart from the seasonal bursts of food abundance and chemical defense of macroalgae, structural complexity of macroalgae could also account for the temporal

variation observed in epiphytic faunal assemblage. The complex microhabitat offered by the epiphytes may be more important for the laterally compressed amphipods than for the dorsoventrally flattened isopods which are well adapted for firmly crawling along the relatively flat thalli of fucoids (Nicotri 1980, Jaconi and Langevin 1996, Pavia *et al.* 1999, Aikins and Kikuchi 2001) so as to lower the chance of being detected by the predators (Gunnill 1982b, Edgar 1983c, Russo 1987). This explains the observation that blooming of amphipods coincided with the flourishing of epiphytes that increased the structural complexity during the reproductive and dieback stages of *Sargassum siliquastrum* in the present study.

In short, the present data supported the assertion that phenology of seaweed can contribute to the temporal fluctuation of faunal abundance in macroalgal community. The life cycle of the faunal species has been found to develop closely with the seaweed phenology (Van Soest 1994). The herbivorous gammaridean amphipods, isopods and gastropods, together with the detritus-feeders caprellidean, harpacticoids and gastropods, were likely to attain their population maxima during the onset of *Sargassum siliquastrum* reproduction and later, the dieback stage as a consequence of the seasonal availability of higher nutritional values and greater quantity of food items in the form of the host macroalgae themselves, the epiphytic algae and their

phyto-detritus. In addition, variation in seaweed chemical defense with seaweed growth stage might contribute synergistically to the blooming of the herbivores and fouling organisms at times of low anti-herbivory and anti-fouling defense during the post-reproductive stage of *Sargassum siliquastrum* in February.

Species richness, in general, reached its peak values in dry season, in particular February and March. Animal species richness was related positively to animal abundance (Simberloff 1978). High species richness during the reproductive and especially the dieback stages of *Sargassum siliquastrum* was probably caused by the occurrence of common groups, notably the amphipods, gastropods and bivalves, in their greatest abundances and diversities during these seaweed growth stages.

4.4.2 Species Composition of Epiphytic Faunal Assemblage in Seaweed Bed of *Sargassum siliquastrum* and its Potential Role as Nursery Grounds

Epiphytic species might show exclusive host specificity, such as a particular algal species (Seed and Boaden 1977, Martin-Smith 1993). Several amphipod species showed distinct food preferences to particular algal species, even though these species would be able to assimilate organic matter from various different food

sources (Pavia *et al* 1999, Karez *et al.* 2000, Adin and Riera 2003). Adult amphipods were found to select algal species that maximized the performance of their relatively immobile offspring (Nicotri 1980, Robertson and Lucas 1983, Poore and Steinberg 1999, Taylor *et al.* 2003, Taylor and Brown 2006). Conlan and Chess (1992), together with Poore and Lowry (1997), showed juvenile amphipods from several genera within the Ampithoidae to remain and develop in close proximity to their mothers on host alga. Poore and Steinberg (1999) indicated the preference of the amphipod *Peramphithoe parmerong* for *Sargassum linearifolium* and *S. vestitum*, among eight algal species and up to 87% of its juveniles remained on the host plant chosen by their mother. Furthermore, Poore (2004) illustrated that the distribution and behaviour of these amphipod juveniles were predictable from differences in the food quality of their host, with most inhabiting the high quality *Sargassum linearfolium* and few emigrating from it. These juveniles acquired highest rates in growth, survival, and onset of reproduction as well as the greatest densities in these two *Sargassum* species despite their relatively not-too-high nutritional values. Herbivores on low nutritional valued hosts compensate for that poor quality by increasing feeding rates so as to maintain nutrient input (Scriber and Slansky 1981, Moran and Arrontes 1994). They became the ubiquitous taxon groups and are considered as residents of the seaweed community. In the present study, these

residents of seaweed bed of *Sargassum siliquastrum* include various species or families of Amphipoda, i.e. families Talitridae, Stenothoidae and Synopiidae; of Gastropoda *Pyrene scripta*, *Mitra* spp. and *Tectarius* spp.; of Bivalvia *Septifer viridis* and *Chama reflexa*. These resident species are likely to be utilizing this seaweed bed as breeding and nesting ground for their juveniles.

Macroalgal bed has been shown to enhance retention of pelagic larvae, thus its settlement and recruitment, by its vegetative structures (Ekman 1983, 1987, Lee 1985, Eckman and Duggins 1991, Irlandi and Peterson 1991, Harvey *et al.* 1995, Jenkins and Sutherland 1997, Rooker and Holt 1997, Boström and Bonsdorff 2000). Settlement and metamorphosis associated with small-scale complexity in physical structure provided by the highly branched macroalgae has been documented for molluscs (Harvey *et al.* 1993, Cáceres-Martínez *et al.* 1994), crustaceans (Herrnkind and Butler 1986), and even fishes (Eggleston 1995). These, in turn, are related with the favourable feeding habitats, the associated trophic conditions (Hadfield and Scheuer 1985, Rice 1986, Laing 1995), as well as the provision of shelter from predators (Ray and Stoner 1994, 1995, Ray-Culp *et al.* 1999) offered by these macroalgae. Queen conch *Strombus gigas* larvae elicited highest metamorphosis and growth rates after settlement on the relatively complex red alga *Neogoniolithon*

strictum and green alga *Dasycladus vermicularis*. These algae were covered with organic and inorganic particulates as food for the conch (Skilleter and Underwood 1993, Stoner *et al.* 1996). In the present study, recruitment of gastropod and bivalve larvae occasionally occurred from December to March, i.e. during the rapid growth, reproductive and dieback stages of *Sargassum siliquastrum*. The supply of larvae, together with the presence of complex structure provided by this brown alga as well as the accumulation of sediments as food might induce the subsequent settlement of these larvae.

Seaweed bed has been recognized as potential nursery and nesting grounds of ecologically and economically important fishery species. The kelp rockfish *Sebastes atrovirens* has been reported to recruit initially to the giant kelp *Macrocystis pyrifera* during summer along the coast of central California when the canopy was the densest (Nelson 2001). Besides, crustaceans of economic importance, such as the Caribbean spiny lobster *Panulirus argus* (Mintz *et al.* 1994) and Blue Crab *Callinectes sapidus* (Epifanio *et al.* 2003), utilized macroalgal bed as nursery habitat for their juveniles. Some groups are transitory and utilize the habitat as a nursery. Adults of some oceanic pelagic fishes occasionally used floating *Sargassum* as a spawning substrate or as a nursery area for their larvae and juveniles (Dooley 1972, Peres 1982, Safran

and Omori 1990, Kingsford 1992, Yeh 1992). The findings from the present study provide good evidence to indicate that the seaweed beds of *Sargassum siliquastrum* are also potential nursery ground of economically important fishery species, notably the mantis shrimp and lobster as well as several fish species, such as the common rockfish *Sebastiscus marmoratus* (Sadovy and Cornish 2000). Stomatopod (i.e. mantis shrimp) and fish juveniles, including those of *Sebastiscus marmoratus, Pelates quadrilineatus, Petroscrites breviceps* and Blennidae, recruited mainly in January and February, during the reproductive and dieback stages of the seaweed. The occurrence of *Petroscrites breviceps* in *Sargassum siliquastrum* bed corroborated the previous findings that juveniles of this species gather around large fronds of *Sargassum* and feed on small crustaceans (Sadovy and Cornish 2000). *Sargassum* crab and lobster juveniles settled during seaweed reproductive and dieback stages, or even in the slow growth stage. In addition, lophogasters are reproductive in December to February (Liu and Wang 2000) and many ovigerous female lophogasters were found in the seaweed bed during this period. Furthermore, nudibranchs were observed to mate and lay eggs on the fronds of *S. siliquastrum*. All these indicate the importance of *S. siliquastrum* bed as a nursery ground, even during its slow growth stage.

4.4.3 Distribution of Epiphytic Fauna in Seaweed Bed of *Sargassum siliquastrum* among Different Localities

Stoner and Greening (1984) illustrated pronounced spatial difference in macrofaunal abundance and species composition of pelagic *Sargassum* between Sargasso Sea and the Gulf Stream. This was probably the consequence of different origins of the North Atlantic circulation or regional differences in nutrient availability that caused variability in epiphyte loads (Conover and Sieburth 1964, Carpenter and Cox 1974), thus offering varying extent of food supply and protection to the associated macrofauna among sites. Moreover, among-site difference in species composition can be attributed to discrepancy in dispersal modes of the associated fauna. Animals with different migration and dispersal abilities will be differentially affected by habitat isolation. Fauna of limited mobility, such as polychaete, experienced limited dispersal among sites. On the other hand, species with greater dispersal abilities, such as pelagic copepod, are able to reach habitats from greater distances (Gunnill 1982b, Virnstein and Curran 1986, Smith and Brumsickle 1989, Bowman *et al.* 2002, Russell *et al.* 2005).

In the present study, epiphytic faunal assemblage and species diversity in LLT and LLS displayed similarity with each other while those at LFN were more different. This pattern was probably due to close proximity of LLT with LLS, which is only 300m apart and thus shared similar epiphytic faunal species with limited dispersal mobility (Nicotri 1980, Robertson and Lucas 1983, Sogard 1989, Poore and Steinberg 1999, Taylor *et al.* 2003, Taylor and Brown 2006). LFN is more distantly (>10 km) located from the two sites and thus consisted of different epiphytic faunal composition. The probability of different circulation origins in causing discrepancy in species composition among sites was not supported as the three sites are subject to the same monsoonal water mass movement (Chen 1992, He *et al.* 1994, Chan 1995, Lee and Chen 2003). On the other hand, some localized coastal circulation may still be present that contributed to isolation of some of the faunal assemblages.

4.4.4 Relationship of Epiphytic Faunal Assemblage with Environmental Factors

Abiotic factors, such as temperature and salinity, were found to play a minor role in structuring epiphytic faunal communities in different species of subtidal macroalgae (Lippert *et al.* 2001) as well as in intertidal rockweed (Sapper and Murray 2003). However, salinity was probably important in the establishment of communities of

invertebrates associated with the green alga *Chara angolensis* in the brackish environment of Imboassica Lagoon in Rio de Janeiro of Brazil, with an associated macroinvertebrate community exhibiting fresh water characteristics far from the sea and another with mesohaline characteristics in the area closest to the sandbar (Albertoni *et al.* 2001). Moreover, temporal dynamics of faunal assemblage might be regulated by solar irradiances, which in turn affected the abundance of epiphytes that served as food source of the fauna (Taylor 1998a). In this present study, the environmental factors, namely temperature, dissolved oxygen and salinity, were unlikely to exert an immediate effect on the associated epiphytic faunal assemblage in seaweed bed of *Sargassum siliquastrum* in terms of abundance and species diversity as the faunal community structure was not significantly related with any of these environmental factors.

4.5 Summary and Conclusion

The structure of epiphytic faunal assemblage was a result of the intermingle of several biotic mechanisms, namely trophic interactions, reproductive biology, and the chemical defense of seaweeds, as previously revealed in sections 4.4.1 and 4.4.2. The peak in total fauna abundance and species richness was due to the seasonal flux of

some common groups, namely gammaridean, caprellidean, isopod, gastropod and harpacticoid, in plenteous number, which is believed to be supported by the seasonal burst of food items, i.e. host macroalgae, the epiphytic algae and their phyto-detritus, of higher quality and quantity, together with the lower seaweed secondary metabolite levels in anti-herbivory and anti-fouling defense during reproductive and dieback stages of *Sargassum siliquastrum*. Synchronization of faunal life cycles with phenology of seaweed *Sargassum siliquastrum* was illustrated in this study. However, no evaluations on the effect of predation pressure and competition in structuring the faunal community were performed. Duffy and Hay (1994) concluded that host plant choice by the amphipod *Amphithoe longimana* and other mesograzers was strongly constrained by predation. Predation might contribute to the differing composition of benthic communities between a temperate-zone seagrass bed and its adjacent sand flat, with significantly more epibenthos inhabiting the seagrass bed where protection from predation was available (Summerson and Peterson 1984). Besides, cannibalism by adult amphipod *Gammarus locusta* on juveniles might have great impact on the population growth associated with macroalgae communities (Christie and Kraufvelin 2004). Moreover, the diets of different epifaunal species were broadly overlapping with the consumption of a variety of microalgae, detrital particles, animal materials and even macroalgae (Zimmerman *et al.* 1979, Van Montfrans *et al.* 1982, Duffy

1990, Edgar 1990). Hence diffuse exploitative competition amongst the epiphytic fauna could be one of the major structuring agents in the faunal assemblage. However, ecological interactions among epifaunal predators and their prey as well as intra- and inter-competition amongst themselves for food and other resources are still mostly under studied. To what extent can biological interactions be strong structuring forces in epiphytic faunal communities remains to be explored (Gunnill 1982a, Edgar 1983c, Stachowicz and Lindquist 1997). The absence of data in some months in the present study might not be able to reflect an implicit picture of temporal variation in faunal assemblage structure. Environmental factors, namely temperature, dissolved oxygen and salinity, were unlikely to exert an immediate effect on the epiphytic faunal assemblage. However, additional monitoring on the physical parameters, such as nutrient loads (Conover and Sieburth 1964, Carpenter and Cox 1974, Stoner and Greening 1984) and solar irradiances, of the water environment might be carried out to further investigate the effects of external abiotic environment on epiphytic faunal assemblage structure in the bed of *Sargassum siliquastrum*. Most importantly, seaweed bed of *Sargassum siliquastrum* was shown to function as site for larval settlement and recruitment, particularly during the rapid growth, reproductive and dieback stages of *Sargassum siliquastrum*. In addition, *Sargassum siliquastrum* bed acted as nursery and nesting grounds for ecologically and economically important

fishery species, notably mantis shrimp, lobster and common rockfish. The essence of *Sargassum siliquastrum* bed as a nursery habitat was also evident even during its slow growth stage.

Table 4.1 The mean (± S.D.) density (m^{-3}) of each epiphytic faunal taxonomic group in each sampling month in LLT. Number in bracket indicates the number of (morpho)species belonging to that particular taxon group. The trophic mode of some taxa is also indicated. Trophic mode abbreviations: f= filter feeder, d= detritus feeder, h= herbivore, o= omnivore, c= carnivore, sv= scavenger.

Taxonomic groups	Trophic mode	Nov-06	Dec-06	Jan-07	Feb-07	Mar-07	May-07	Jun-07	Aug-07	Sep-07	Oct-07	Nov-07	Dec-07	Feb-08
Amphipoda														
Gammaridean	h													
Talitridae (4)		0.93 ± 1.27	0.71 ± 0.65	0.98 ± 1.13	0.19 ± 0.20	0.65 ± 0.72	6.57 ± 12.34	0.00 ± 0.00	0.38 ± 0.73	1.01 ± 1.32	2.90 ± 4.76	1.36 ± 1.60	0.59 ± 0.83	3.61 ± 3.21
Stenothoidae (6)		0.51 ± 0.61	0.09 ± 0.18	0.45 ± 0.59	0.51 ± 0.45	0.46 ± 0.55	4.63 ± 6.93	0.00 ± 0.00	0.15 ± 0.37	0.96 ± 1.28	1.37 ± 1.53	1.42 ± 1.32	1.49 ± 1.87	3.67 ± 5.14
Podoceridae (3)		0.37 ± 0.90	0.05 ± 0.16	0.08 ± 0.24	0.08 ± 0.12	1.01 ± 0.78	0.00 ± 0.00	0.00 ± 0.00	0.45 ± 1.11	0.00 ± 0.00	0.74 ± 1.13	2.05 ± 3.97	3.79 ± 1.58	12.71 ± 9.13
Maxillipedidae (4)		0.54 ± 1.02	0.00 ± 0.00	0.10 ± 0.30	0.00 ± 0.00	0.10 ± 0.22	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Synopiidae (2)		0.00 ± 0.00	0.12 ± 0.26	0.43 ± 0.76	0.20 ± 0.20	0.29 ± 0.27	0.24 ± 0.53	0.00 ± 0.00	0.05 ± 0.12	0.17 ± 0.35	0.00 ± 0.00	0.53 ± 1.09	0.00 ± 0.00	13.90 ± 10.37
Dogielinotidae (1)		0.00 ± 0.00	0.02 ± 0.07	0.00 ± 0.00	0.04 ± 0.11	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.18 ± 0.55	0.00 ± 0.00
Amphithoidae														
Amphithoe spp.	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	3.20 ± 3.34	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.21	0.00 ± 0.00	0.26 ± 0.77	0.06 ± 0.12	0.96 ± 1.48
Dexaminidae (2)		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.31 ± 0.70	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.15	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	4.64 ± 3.53
Corophiidae (2)		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Corophium spp.	d	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.10	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Aikaliv spp.	d	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.23 ± 0.32	0.00 ± 0.00	0.00 ± 0.00	0.23 ± 0.55	0.00 ± 0.00	0.00 ± 0.00	0.25 ± 0.41	1.54 ± 1.07	12.99 ± 7.80
Ampeliscidae (2)														
Byblis kallarthro		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.43 ± 1.04	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Ampelisca spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.77 ± 4.95
Melitidae (2)	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Gammaridean juvenile		2.55 ± 2.04	3.29 ± 5.05	4.31 ± 3.29	10.54 ± 6.37	18.93 ± 11.64	52.56 ± 44.50	3.58 ± 5.97	0.51 ± 0.87	4.35 ± 3.19	7.26 ± 4.03	9.55 ± 7.18	31.91 ± 17.07	429.03 ± 219.78
Caprellidean	h	1.52 ± 3.57	1.06 ± 2.09	0.54 ± 0.79	3.25 ± 3.34	1.95 ± 2.13	3.56 ± 6.83	0.00 ± 0.00	0.82 ± 1.09	0.94 ± 0.86	0.98 ± 1.30	1.06 ± 0.68	3.90 ± 4.63	26.95 ± 28.05
Hyperidean														
Oxycephalidae	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Polychaeta (44)	c, h, d	1.78 ± 3.53	0.52 ± 0.57	0.55 ± 0.66	1.58 ± 1.40	2.69 ± 1.43	1.85 ± 1.48	0.00 ± 0.00	5.03 ± 7.52	0.19 ± 0.28	0.00 ± 0.00	0.82 ± 1.06	3.20 ± 5.01	10.76 ± 14.03
Tubeworm	f													
Hydroides spp.		1.80 ± 3.53	0.00 ± 0.00	0.20 ± 0.35	0.14 ± 0.20	0.04 ± 0.10	0.00 ± 0.00	0.69 ± 1.68	0.00 ± 0.00	0.06 ± 0.19	1.77 ± 2.18	5.76 ± 6.04	0.54 ± 0.72	0.25 ± 0.49
Spirorbis spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.11	0.00 ± 0.00	0.79 ± 1.76	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Decapoda														
Brachyura														
Menaethius monoceros	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.03 ± 0.08	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Majidae juvenile	h	0.00 ± 0.00	0.02 ± 0.07	0.03 ± 0.10	0.01 ± 0.04	0.20 ± 0.44	1.43 ± 2.13	0.00 ± 0.00	0.00 ± 0.00	0.37 ± 0.76	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Xanthidae														
Lagore spp.	c	0.00 ± 0.00	0.05 ± 0.14	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Hymenicus spp.	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Zyrnicus spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Lobster juvenile	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.07	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.12 ± 0.35
Anomura														
Porcellanidae juvenile														
Liosporcellana quadrilobata	sv, d	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.18 ± 0.53
Hermit crab	h, d	0.22 ± 0.46	0.37 ± 0.89	0.32 ± 0.46	1.55 ± 1.46	0.34 ± 0.22	3.05 ± 2.40	0.27 ± 0.66	2.11 ± 5.17	0.12 ± 0.24	0.20 ± 0.46	0.57 ± 0.97	2.09 ± 3.70	4.04 ± 4.49
Macrura														
Penaeid shrimp	c	0.34 ± 1.02	0.04 ± 0.13	0.00 ± 0.00	0.01 ± 0.04	0.10 ± 0.22	0.00 ± 0.00	0.00 ± 0.00	1.11 ± 2.57	0.05 ± 0.15	0.25 ± 0.51	0.00 ± 0.00	0.05 ± 0.16	0.32 ± 0.50
Barnacle	f													
Chthamalus spp.		8.83 ± 13.81	3.09 ± 4.86	1.11 ± 1.39	5.21 ± 7.63	7.57 ± 5.73	70.24 ± 20.34	4.57 ± 7.94	4.65 ± 7.28	2.10 ± 2.01	1.80 ± 1.92	0.82 ± 1.23	3.33 ± 3.74	33.08 ± 49.58
Cirripedia larvae		0.19 ± 0.37	0.00 ± 0.00	0.03 ± 0.10	0.03 ± 0.09	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 1.41	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Copepoda														
Calanoida	f													
Temora turbinata		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.36 ± 3.33	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Labidocera mirum		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Harpacticoida	d	0.00 ± 0.00	1.28 ± 1.44	1.92 ± 2.80	1.20 ± 1.38	0.27 ± 0.61	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.46 ± 0.73	0.00 ± 0.00	0.00 ± 0.00	1.28 ± 1.59	1.66 ± 4.98
Echinodermata														
Brittle star														
Ophiothrix spp.	sv, d	2.37 ± 4.40	0.70 ± 1.05	0.20 ± 0.35	0.16 ± 0.25	0.20 ± 0.27	1.76 ± 1.79	9.17 ± 11.65	3.76 ± 5.37	3.47 ± 6.36	1.61 ± 2.86	0.45 ± 0.93	1.14 ± 2.87	5.08 ± 6.55
Sea urchin														
Salamacis dussumieri	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.19 ± 0.46	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.05	0.00 ± 0.00
Anthocidaris crassispina	o	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.13 ± 0.40
Temnopleurus toreumaticus	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Starfish larvae		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.19	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Fish larva & juvenile														
Sebastiscus marmoratus	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.13	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.07 ± 0.22
Blenniidae	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Pelates quadrilineatus	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Petroscirtes breviceps	o	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

Table 4.1 (cont'd)

Taxonomic groups	Trophic mode	Nov-06	Dec-06	Jan-07	Feb-07	Mar-07	May-07	Jun-07	Aug-07	Sep-07	Oct-07	Nov-07	Dec-07	Feb-08
Mollusca														
Gastropoda														
Prosobranchia														
Pyrene scripta	d, h	0.59 ± 1.78	0.68 ± 0.64	1.16 ± 0.68	1.03 ± 0.68	0.63 ± 0.59	2.19 ± 2.26	0.91 ± 1.12	0.63 ± 1.27	0.56 ± 0.46	2.75 ± 2.38	2.13 ± 1.23	2.75 ± 3.70	2.29 ± 2.68
Pyrene spp.	d, h	1.38 ± 3.01	1.00 ± 1.29	0.91 ± 1.04	0.36 ± 0.28	0.87 ± 1.41	9.53 ± 10.82	4.22 ± 9.27	0.68 ± 1.14	1.07 ± 1.02	0.40 ± 0.65	0.44 ± 0.69	0.42 ± 0.63	7.13 ± 6.42
Mitra spp.	d	0.14 ± 0.41	0.70 ± 1.41	0.11 ± 0.22	0.85 ± 0.99	2.09 ± 2.99	0.68 ± 1.07	0.00 ± 0.00	0.23 ± 0.55	0.97 ± 2.08	0.00 ± 0.00	0.07 ± 0.15	0.45 ± 0.80	2.16 ± 2.26
Mitra rugosum	d, c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Tectarius sp.1		2.74 ± 4.24	0.02 ± 0.07	0.20 ± 0.40	0.00 ± 0.00	0.29 ± 0.66	0.00 ± 0.00	3.92 ± 5.77	1.66 ± 2.52	0.68 ± 0.93	0.15 ± 0.32	0.00 ± 0.00	0.06 ± 0.17	3.32 ± 9.97
Tectarius sp.2		0.39 ± 1.18	0.06 ± 0.13	0.01 ± 0.04	0.31 ± 0.29	0.47 ± 0.47	1.32 ± 1.80	1.41 ± 3.09	0.00 ± 0.00	0.32 ± 0.81	0.00 ± 0.00	0.26 ± 0.64	1.01 ± 2.05	3.13 ± 3.33
Marginella spp.	c	0.07 ± 0.20	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.23 ± 0.55	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.32 ± 0.97	0.00 ± 0.00
Cancellaria spp.	h	0.50 ± 0.90	0.05 ± 0.14	0.02 ± 0.07	0.09 ± 0.17	0.10 ± 0.22	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Lunella coronata		0.00 ± 0.00	0.13 ± 0.27	0.00 ± 0.00	0.34 ± 0.46	0.00 ± 0.00	0.80 ± 0.84	3.92 ± 6.48	0.00 ± 0.00	0.05 ± 0.15	0.00 ± 0.00	0.00 ± 0.00	0.25 ± 0.49	
Lunella spp. juvenile		0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.07	0.02 ± 0.05	0.10 ± 0.22	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cerithidea spp.	h	0.00 ± 0.00	0.00 ± 0.00	0.06 ± 0.14	0.05 ± 0.11	0.39 ± 0.63	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.36 ± 0.79	0.03 ± 0.10	0.28 ± 0.56
Monodonta nemoides	h	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.14	0.00 ± 0.00	0.10 ± 0.22	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Astraea rhodostoma	h	0.00 ± 0.00	0.00 ± 0.00	0.09 ± 0.20	0.18 ± 0.23	0.00 ± 0.00	0.41 ± 0.58	0.13 ± 0.33	0.20 ± 0.37	0.24 ± 0.71	0.24 ± 0.71	0.18 ± 0.40	0.06 ± 0.18	2.33 ± 6.31
Littorina spp.	h	0.00 ± 0.00	0.00 ± 0.00	0.14 ± 0.34	0.31 ± 0.67	0.24 ± 0.42	0.63 ± 0.91	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.39 ± 0.62	0.48 ± 0.58	0.29 ± 0.54	0.00 ± 0.00
Morula spp.		0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.07	0.35 ± 0.29	0.20 ± 0.44	3.00 ± 4.12	0.00 ± 0.00	0.21 ± 0.52	0.19 ± 0.38	0.29 ± 0.70	0.32 ± 0.49	0.70 ± 1.11	2.59 ± 4.87
Oliva spp.	sv, c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.05	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Tectus conus		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.05	0.04 ± 0.10	2.56 ± 5.26	0.98 ± 1.82	0.21 ± 0.52	0.09 ± 0.26	0.03 ± 0.10	0.00 ± 0.00	0.16 ± 0.27	16.15 ± 17.59
Tectus pyramis	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.48 ± 1.06	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cronia margaritula		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.24	0.49 ± 0.69	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.15 ± 0.38	0.00 ± 0.00	0.00 ± 0.00
Taenitella spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.22	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Crepidula spp.	f	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.71 ± 0.98	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.16	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cantharus spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	8.42 ± 6.06	0.00 ± 0.00	0.00 ± 0.00	0.54 ± 1.40	0.00 ± 0.00	0.11 ± 0.32	0.31 ± 0.83	1.10 ± 2.01
Epitonium spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.48 ± 1.06	0.00 ± 0.00	0.00 ± 0.00	0.14 ± 0.41	0.12 ± 0.35	0.00 ± 0.00	0.24 ± 0.47	8.33 ± 9.33
Thais luteostoma		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.03 ± 0.10	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Nassacmea Schrenkii		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Diodora ticaonica	f	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Halcis spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cypraea gracilis	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cypraea arabicus	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Telescopium spp. juvenile		0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.07	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Gastropoda juvenile	f	0.00 ± 0.00	0.45 ± 0.83	0.07 ± 0.21	0.15 ± 0.22	0.86 ± 0.53	0.63 ± 0.91	2.00 ± 3.21	0.26 ± 0.51	0.00 ± 0.00	0.46 ± 1.10	1.27 ± 1.41	9.37 ± 8.85	17.09 ± 14.97
Nudibranchia														
Aplysia juliana	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.03 ± 0.10	0.00 ± 0.00
Chromodoris pallescens	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.39 ± 0.88	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Bivalvia	f													
Ostrea cucullata		0.00 ± 0.00	0.21 ± 0.34	0.12 ± 0.24	0.24 ± 0.27	0.00 ± 0.00	0.00 ± 0.00	0.69 ± 1.68	1.27 ± 2.53	0.06 ± 0.19	0.00 ± 0.00	0.05 ± 0.16	0.00 ± 0.00	0.27 ± 0.53
Isognomon spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Siliqua spp.		0.00 ± 0.00	0.00 ± 0.00	0.03 ± 0.08	0.02 ± 0.05	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.45 ± 1.11	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cardita leana		0.07 ± 0.20	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.16	0.00 ± 0.00	0.00 ± 0.00
Perna spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Pinctada spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Spondylus sinensis		0.09 ± 0.27	0.07 ± 0.21	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Barbatia obliqua		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Barbatia sp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Barbatia spp. juvenile		0.00 ± 0.00	0.04 ± 0.12	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Septifer bilocularis		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Septifer virgatus		0.39 ± 1.18	0.04 ± 0.13	0.06 ± 0.17	0.08 ± 0.15	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.45 ± 1.11	0.05 ± 0.15	0.11 ± 0.32	0.03 ± 0.10	0.00 ± 0.00	2.45 ± 5.07
Chama reflexa		0.00 ± 0.00	0.02 ± 0.07	0.12 ± 0.20	0.06 ± 0.09	5.35 ± 6.29	0.00 ± 0.00	0.23 ± 0.55	0.00 ± 0.00	0.19 ± 0.42	0.17 ± 0.37	0.28 ± 0.50	0.23 ± 0.70	31.91 ± 78.55
Placamen calophylla		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mytilidae sp.1 juvenile		0.90 ± 2.69	0.26 ± 0.39	0.30 ± 0.59	0.14 ± 0.17	3.75 ± 5.16	1.76 ± 2.43	0.00 ± 0.00	0.00 ± 0.00	0.20 ± 0.43	0.00 ± 0.00	0.05 ± 0.16	0.19 ± 0.57	0.00 ± 0.00
Mytilidae sp.2 juvenile		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.06 ± 2.59	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Nuculidae		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.12	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mytilacea														
Lophogaster pacificus	c	0.14 ± 0.30	0.36 ± 0.60	0.23 ± 0.38	0.12 ± 0.14	0.19 ± 0.27	0.49 ± 0.71	0.00 ± 0.00	0.61 ± 1.10	0.55 ± 1.29	0.03 ± 0.10	0.21 ± 0.40	0.13 ± 0.27	0.00 ± 0.00
Sinella vulgaris	o	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.44 ± 0.68	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Unidentified mysis	o	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.16	0.00 ± 0.00	0.14 ± 0.42	0.00 ± 0.00
Mysidae Juvenile	o	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.35 ± 0.70	0.00 ± 0.00	0.24 ± 0.47	0.00 ± 0.00	0.00 ± 0.00
Cnidaria														
Hydroid polyp	c	0.00 ± 0.00	0.90 ± 2.18	0.00 ± 0.00	0.07 ± 0.13	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.16 ± 0.54	0.98 ± 1.98	0.00 ± 0.00
Isopoda	h	1.03 ± 2.10	1.77 ± 3.34	1.02 ± 1.02	0.59 ± 0.73	0.19 ± 0.27	2.80 ± 3.34	0.82 ± 0.99	1.43 ± 2.01	0.82 ± 1.38	0.42 ± 0.89	0.00 ± 0.00	0.71 ± 0.88	2.44 ± 4.87
Chiton	h	0.50 ± 0.90	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.06	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.13 ± 0.40
Sea Anemone	c	0.00 ± 0.00	0.05 ± 0.14	0.00 ± 0.00	0.00 ± 0.00	0.54 ± 1.21	0.17 ± 0.39	0.00 ± 0.00	0.00 ± 0.00	0.17 ± 0.34	0.12 ± 0.35	0.00 ± 0.00	0.05 ± 0.16	0.96 ± 1.98
Stomatopoda, Mantis shrimp	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.13 ± 0.40
Sipuncula, Peanut worm	d	1.18 ± 3.55	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.19 ± 0.42	0.00 ± 0.00	0.00 ± 0.00	0.86 ± 1.77	0.27 ± 0.53
Sponge	f	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Others, e.g. insecta		0.00 ± 0.00	0.00 ± 0.00	0.12 ± 0.24	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Total		31.26 ± 32.14	18.25 ± 14.75	16.12 ± 8.77	50.20 ± 19.40	46.69 ± 16.38	187.43 ± 88.66	57.90 ± 24.97	30.96 ± 28.63	22.30 ± 8.40	25.01 ± 9.15	31.68 ± 10.29	74.40 ± 35.27	638.72 ± 199.91

Table 4.2 The mean (± S.D.) density (m^{-3}) of each epiphytic faunal taxonomic group in each sampling month in LLS. Number in bracket indicates the number of (morpho)species belonging to that particular taxon group. The trophic mode of some taxa is also indicated. Trophic mode abbreviations as in Table 4.1.

Taxonomic groups	Trophic mode	Nov-06	Dec-06	Jan-07	Feb-07	Apr-07	May-07	Jun-07	Oct-07	Nov-07	Dec-07	Feb-08
Amphipoda												
Gammaridean	h											
Talitridae (4)		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	2.07 ± 4.63	0.00 ± 0.00	0.00 ± 0.00	0.70 ± 0.95	1.16 ± 1.42	2.43 ± 2.77	1.67 ± 2.80
Stenothoidae (6)		0.00 ± 0.00	0.57 ± 1.40	0.46 ± 1.54	1.52 ± 2.86	0.92 ± 2.06	0.00 ± 0.00	0.44 ± 0.68	0.47 ± 1.23	1.01 ± 1.11	5.34 ± 6.46	1.19 ± 1.64
Podoceridae (3)		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.16 ± 0.47	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.90 ± 1.19	0.37 ± 0.77	0.64 ± 1.45	2.49 ± 2.92
Maxillipidae (4)		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.15	0.00 ± 0.00	0.00 ± 0.00
Synopiidae (2)		0.00 ± 0.00	0.67 ± 1.65	0.00 ± 0.00	0.16 ± 0.47	0.33 ± 0.74	0.37 ± 0.82	0.00 ± 0.00	0.00 ± 0.00	0.16 ± 0.47	1.99 ± 2.96	3.55 ± 3.71
Dogielinotidae (1)		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Amphithoidae												
Ampithoe spp.	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.42 ± 0.86	0.00 ± 0.00	2.07 ± 1.97
Dexaminidae (2)		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.12 ± 0.37	3.13 ± 4.03
Corophiidae (2)		±	±	±	±	±	±	±	±	±	±	±
Corophium spp.	d	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Aliculoides spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.65 ± 1.02	0.41 ± 0.93	0.00 ± 0.00	0.00 ± 0.00	0.36 ± 0.62	0.32 ± 0.61	1.21 ± 1.55	1.92 ± 2.71
Ampeliscidae (2)	d											
Byblis kullerthros		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.21 ± 0.42
Ampelisca spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.17 ± 0.51
Melitidae (2)	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.19 ± 1.52	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Gammaridean juvenile		3.09 ± 3.68	3.23 ± 3.79	9.30 ± 11.07	19.03 ± 15.49	19.53 ± 19.66	5.71 ± 3.24	0.00 ± 0.00	7.74 ± 3.55	5.33 ± 3.11	127.06 ± 103.75	78.87 ± 21.61
Caprellidean	h	5.38 ± 14.04	0.00 ± 0.00	0.00 ± 0.00	2.52 ± 3.75	41.31 ± 56.74	0.91 ± 1.44	0.00 ± 0.00	0.16 ± 0.43	0.15 ± 0.31	10.73 ± 8.03	17.58 ± 12.13
Hyperiidean												
Oxycephalidae	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Polychaeta (44)	c, h, d	11.11 ± 14.21	1.15 ± 1.84	6.82 ± 7.88	2.93 ± 4.33	2.83 ± 1.85	1.31 ± 1.22	0.74 ± 0.59	2.49 ± 4.45	0.42 ± 0.79	2.40 ± 3.64	0.89 ± 2.29
Tubeworm	f											
Hydroides spp.		2.27 ± 3.76	0.00 ± 0.00	1.73 ± 4.08	0.22 ± 0.66	0.42 ± 0.94	0.37 ± 0.82	0.16 ± 0.40	1.56 ± 4.14	0.05 ± 0.15	0.17 ± 0.50	0.00 ± 0.00
Spirorbis spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Decapoda												
Brachyura												
Menaethius monoceros	h	0.00 ± 0.00	0.00 ± 0.00	1.46 ± 3.34	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.06 ± 0.17	0.80 ± 1.28
Majidae juvenile	h	0.43 ± 1.36	0.00 ± 0.00	1.16 ± 3.86	0.25 ± 0.74	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.61 ± 2.09	0.15 ± 0.29	0.35 ± 0.61	0.00 ± 0.00
Xanthidae												
Liagore spp.	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Phymodius spp.	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.42 ± 0.94	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Dynomene spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.25 ± 0.74	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Lobster juvenile	c	0.64 ± 2.03	0.57 ± 1.40	0.76 ± 2.52	0.44 ± 0.93	0.77 ± 1.72	0.00 ± 0.00	0.00 ± 0.00	1.56 ± 4.14	0.06 ± 0.17	0.00 ± 0.00	0.24 ± 0.73
Anomura												
Porcellanidae juvenile												
Lissoporcellana quadrilobata	sv, d	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.77 ± 2.30
Hermit crab	h, d	2.22 ± 3.68	7.03 ± 6.54	6.61 ± 8.60	2.85 ± 4.32	9.30 ± 6.04	2.20 ± 2.24	2.16 ± 3.17	2.65 ± 3.80	1.59 ± 1.56	4.25 ± 3.73	5.08 ± 4.62
Macrura												
Penaeid shrimp	c	0.55 ± 1.73	0.43 ± 1.05	1.19 ± 2.89	1.84 ± 4.25	0.77 ± 1.72	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.15 ± 0.46	1.66 ± 3.69	0.68 ± 0.88
Barnacle	f											
Chthamalus spp.		19.57 ± 31.46	4.42 ± 5.51	43.32 ± 63.72	4.44 ± 4.04	7.45 ± 11.39	9.16 ± 10.16	3.24 ± 3.05	0.71 ± 1.22	0.00 ± 0.00	0.00 ± 0.00	0.45 ± 0.90
Cirripedia larvae		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Copepoda												
Calanoida	f											
Temora turbinata		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Labidocera minuta		0.00 ± 0.00	0.73 ± 1.78	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Harpacticoida	d	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.16 ± 0.47	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Echinodermata												
Brittle star												
Ophiothrix spp.	sv, d	1.08 ± 2.55	0.67 ± 1.65	2.91 ± 5.04	0.00 ± 0.00	1.18 ± 1.74	0.25 ± 0.56	0.00 ± 0.00	1.73 ± 4.09	0.16 ± 0.47	0.11 ± 0.33	0.00 ± 0.00
Sea urchin												
Salamacis dussumieri	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.52 ± 0.93	0.00 ± 0.00	0.06 ± 0.17	0.00 ± 0.00
Anthocidaris crassispina	o	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.31 ± 0.94	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Temnopleurus hemantacus	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.60 ± 1.20	0.33 ± 0.74	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Starfish larvae		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Fish larva & juvenile												
Sebastiscus marmoratus	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.11	0.00 ± 0.00
Blenniidae	h	0.00 ± 0.00	0.00 ± 0.00	0.42 ± 1.38	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Pelates quadrilineatus	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Petroscirtes breviceps	o	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

Table 4.2 (cont'd)

Taxonomic groups	Trophic mode	Nov-06	Dec-06	Jan-07	Feb-07	Apr-07	May-07	Jun-07	Oct-07	Nov-07	Dec-07	Feb-08
Mollusca												
Gastropoda												
Prosobranchia												
Pyrene scripta	d, h	12.01 ± 6.65	6.76 ± 8.02	7.09 ± 8.82	3.23 ± 3.07	5.13 ± 6.33	2.94 ± 2.43	4.15 ± 3.41	6.58 ± 7.94	6.65 ± 3.15	8.95 ± 8.29	11.26 ± 5.35
Pyrene spp.	d, h	5.64 ± 6.76	5.08 ± 5.73	8.33 ± 11.45	1.36 ± 2.74	0.74 ± 1.03	0.73 ± 1.63	0.49 ± 0.82	7.46 ± 8.33	2.85 ± 2.50	8.02 ± 18.69	5.69 ± 7.95
Mitra spp.	d	0.86 ± 2.73	6.32 ± 7.45	8.36 ± 10.03	1.45 ± 2.94	0.00 ± 0.00	0.17 ± 0.37	0.63 ± 1.13	0.85 ± 1.46	0.35 ± 0.58	0.60 ± 0.81	3.01 ± 3.04
Mitra rugosum	d, e	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Tectarius sp.1		3.83 ± 8.33	3.78 ± 5.89	3.49 ± 5.04	0.00 ± 0.00	0.00 ± 0.00	0.62 ± 0.87	0.00 ± 0.00	0.99 ± 1.34	0.27 ± 0.54	1.24 ± 2.68	0.34 ± 0.78
Tectarius sp.2		0.00 ± 0.00	1.71 ± 4.19	0.00 ± 0.00	1.42 ± 1.83	0.92 ± 2.06	0.00 ± 0.00	0.23 ± 0.57	1.81 ± 2.57	0.69 ± 1.54	0.26 ± 0.56	0.45 ± 0.54
Marginella spp.	c	1.48 ± 4.68	0.00 ± 0.00	0.00 ± 0.00	0.31 ± 0.94	0.42 ± 0.94	0.00 ± 0.00	0.00 ± 0.00	0.38 ± 1.02	0.00 ± 0.00	0.00 ± 0.00	0.31 ± 0.70
Cancellaria spp.	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Lunella coronata		0.55 ± 1.73	0.57 ± 1.40	0.58 ± 1.93	0.00 ± 0.00	0.87 ± 1.20	0.00 ± 0.00	0.16 ± 0.40	0.68 ± 1.80	0.00 ± 0.00	0.11 ± 0.33	0.00 ± 0.00
Lunella spp. juvenile		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cerithidea spp.	h	1.08 ± 2.55	0.00 ± 0.00	0.58 ± 1.93	0.54 ± 1.08	0.00 ± 0.00	0.38 ± 0.84	0.00 ± 0.00	2.10 ± 3.60	0.00 ± 0.00	0.04 ± 0.11	0.11 ± 0.34
Monodonta neritoides	h	0.55 ± 1.73	1.84 ± 3.34	0.42 ± 1.38	0.00 ± 0.00	0.00 ± 0.00	0.84 ± 0.81	1.07 ± 1.43	0.47 ± 1.23	0.00 ± 0.00	0.88 ± 1.76	0.84 ± 1.98
Astraea rhodostoma	h	3.15 ± 5.53	0.69 ± 1.69	0.88 ± 2.93	0.00 ± 0.00	1.66 ± 3.70	0.00 ± 0.00	0.21 ± 0.51	1.31 ± 1.94	0.00 ± 0.00	1.04 ± 1.70	0.00 ± 0.00
Littorina spp.	h	0.00 ± 0.00	3.09 ± 3.06	0.35 ± 1.17	0.49 ± 1.47	0.33 ± 0.74	0.00 ± 0.00	0.70 ± 0.83	1.55 ± 2.93	0.37 ± 0.59	0.79 ± 1.27	2.53 ± 3.83
Morula spp.		5.44 ± 5.33	1.14 ± 2.79	0.46 ± 1.54	1.18 ± 1.61	0.00 ± 0.00	0.22 ± 0.50	0.23 ± 0.57	4.80 ± 5.47	0.34 ± 0.43	0.67 ± 1.88	0.09 ± 0.26
Oliva spp.	sv, c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Tectus conus		2.59 ± 8.19	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.46 ± 1.03	0.00 ± 0.00	0.00 ± 0.00	1.74 ± 3.18	0.27 ± 0.59	0.95 ± 2.73	0.27 ± 0.59
Tectus pyramis	h	0.00 ± 0.00	0.00 ± 0.00	0.35 ± 1.17	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.65 ± 1.96
Cronia margaritacola		5.30 ± 9.35	2.60 ± 3.26	4.66 ± 5.73	0.82 ± 1.79	5.30 ± 3.33	0.37 ± 0.82	0.23 ± 0.57	2.03 ± 2.80	0.05 ± 0.15	1.33 ± 2.38	0.24 ± 0.48
Turritella spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Crepidula spp.	f	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.15 ± 1.41	1.15 ± 3.05	0.18 ± 0.35	0.00 ± 0.00	0.00 ± 0.00
Cantharus spp.		0.00 ± 0.00	1.14 ± 1.81	1.51 ± 3.91	0.00 ± 0.00	0.41 ± 0.93	0.25 ± 0.56	0.90 ± 1.69	6.05 ± 8.56	0.70 ± 1.10	0.41 ± 0.70	0.26 ± 0.77
Epitonium spp.		0.00 ± 0.00	0.00 ± 0.00	0.42 ± 1.38	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.47 ± 1.14	1.40 ± 3.69	0.00 ± 0.00	0.63 ± 1.89	0.44 ± 0.77
Thais luteostoma		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.54 ± 1.44	0.06 ± 0.19	0.00 ± 0.00	0.00 ± 0.00
Neotrigonia Schreiberi		0.43 ± 1.36	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Diodora tecomica	f	0.94 ± 2.96	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Balcis spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.18 ± 0.44	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cypraea gracilis	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.41 ± 0.93	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.22 ± 0.66	0.78 ± 1.95
Cypraea arabicus	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.11	0.00 ± 0.00
Telescopium spp. juvenile		0.00 ± 0.00	0.00 ± 0.00	0.42 ± 1.38	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.20 ± 0.48	0.68 ± 1.80	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Gastropoda juvenile	f	0.00 ± 0.00	0.00 ± 0.00	0.42 ± 1.38	0.00 ± 0.00	0.00 ± 0.00	1.30 ± 2.47	0.00 ± 0.00	0.00 ± 0.00	0.39 ± 0.83	0.04 ± 0.11	0.00 ± 0.00
Nudibranchia												
Aplysia juliana	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.41 ± 0.93	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Chromodoris pallescens	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.22 ± 0.50	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Bivalvia	f											
Ostrea cucullata		2.45 ± 3.60	0.43 ± 1.05	3.41 ± 7.66	1.66 ± 2.19	0.33 ± 0.74	0.45 ± 1.00	0.00 ± 0.00	0.00 ± 0.00	0.33 ± 0.76	0.00 ± 0.00	0.00 ± 0.00
Isognomon spp.		0.43 ± 1.36	0.00 ± 0.00	1.04 ± 2.34	0.82 ± 1.25	0.00 ± 0.00	0.00 ± 0.00	0.79 ± 1.09	0.00 ± 0.00	0.52 ± 1.57	0.22 ± 0.44	0.50 ± 1.16
Siliqua spp.		0.55 ± 1.73	0.73 ± 1.78	0.84 ± 1.88	0.00 ± 0.00	1.30 ± 1.90	0.39 ± 0.54	0.00 ± 0.00	0.16 ± 0.43	0.32 ± 0.78	0.00 ± 0.00	0.26 ± 0.77
Cardita leana		0.43 ± 1.36	0.47 ± 1.14	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.23 ± 0.57	0.34 ± 0.90	0.13 ± 0.38	0.11 ± 0.33	0.11 ± 0.34
Pteria spp.		0.64 ± 2.03	0.69 ± 1.69	1.31 ± 2.94	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	2.11 ± 4.15	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Pinctada spp.		0.00 ± 0.00	0.00 ± 0.00	0.35 ± 1.17	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Spondylus sinensis		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.38 ± 0.84	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Barbatia obliqua		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.16 ± 0.40	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Barbatia sp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Barbatia spp. juvenile		0.00 ± 0.00	0.00 ± 0.00	0.58 ± 1.93	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Septifer bilocularis		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Septifer virdis		2.14 ± 3.53	0.47 ± 1.14	1.46 ± 3.34	0.80 ± 1.21	0.77 ± 1.72	0.00 ± 0.00	0.00 ± 0.00	0.15 ± 0.29	0.11 ± 0.33	0.23 ± 0.68	
Chama reflexa		1.78 ± 3.24	0.43 ± 1.05	7.25 ± 10.07	0.85 ± 1.28	0.79 ± 1.11	0.47 ± 0.65	3.30 ± 4.48	1.95 ± 4.09	0.15 ± 0.29	0.63 ± 1.89	0.23 ± 0.46
Placamen calophylla		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mytilidae sp.1 juvenile		2.07 ± 4.82	2.45 ± 4.84	3.90 ± 7.47	0.29 ± 0.86	0.00 ± 0.00	0.95 ± 1.30	0.33 ± 0.80	0.54 ± 1.44	0.19 ± 0.57	0.33 ± 0.98	0.00 ± 0.00
Mytilidae sp.2 juvenile		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Nuculidae		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mysidacea												
Lophogaster pacificus	c	8.08 ± 7.70	0.00 ± 0.00	3.56 ± 6.30	0.56 ± 1.12	1.69 ± 2.33	0.00 ± 0.00	0.00 ± 0.00	1.22 ± 1.85	0.42 ± 0.95	0.24 ± 0.55	0.65 ± 1.11
Sirella vulgaris	o	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.58 ± 0.81	0.16 ± 0.40	0.00 ± 0.00	0.00 ± 0.00	0.46 ± 1.15	0.65 ± 1.96
Unidentified mysis	o	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	±	±
Mysidae Juvenile	o	0.00 ± 0.00	0.47 ± 1.14	0.58 ± 1.93	0.00 ± 0.00	0.46 ± 1.03	0.76 ± 1.69	1.06 ± 1.30	3.09 ± 4.84	0.51 ± 0.90	2.36 ± 5.58	0.00 ± 0.00
Cnidaria												
Hydroid polyp	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Isopoda	h	4.11 ± 7.45	1.99 ± 2.20	2.43 ± 3.48	0.99 ± 1.60	0.46 ± 1.03	1.75 ± 2.37	0.00 ± 0.00	2.87 ± 1.84	0.41 ± 0.54	1.88 ± 2.61	0.11 ± 0.34
Chiton	h	0.00 ± 0.00	0.00 ± 0.00	0.73 ± 2.42	0.00 ± 0.00	0.41 ± 0.93	0.00 ± 0.00	0.23 ± 0.57	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Sea Anemone	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.62 ± 1.75	0.00 ± 0.00
Stomatopoda, Mantis shrimp	c	0.00 ± 0.00	0.00 ± 0.00	0.46 ± 1.54	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Sipuncula, Peanut worm	d	0.00 ± 0.00	0.00 ± 0.00	0.42 ± 1.38	0.00 ± 0.00	1.19 ± 1.74	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.21 ± 0.43
Sponge	f	0.73 ± 1.57	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.12 ± 0.37	0.00 ± 0.00
Others, e.g. insecta		0.00 ± 0.00	0.00 ± 0.00	0.89 ± 2.95	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Total		113.59 ± 60.87	62.29 ± 32.23	140.68 ± 118.19	55.09 ± 27.83	112.93 ± 84.32	34.04 ± 8.47	21.08 ± 16.12	78.45 ± 33.41	27.82 ± 8.97	191.91 ± 128.50	152.12 ± 12.80

Table 4.3 The mean (± S.D.) density (m^{-3}) of each epiphytic faunal taxonomic group in each sampling month in LFN. Number in bracket indicates the number of (morpho)species belonging to that particular taxon group. The trophic mode of some taxa is also indicated. Trophic mode abbreviations as in Table 4.1.

Taxonomic groups	Trophic mode	Nov-06	Dec-06	Jan-07	Feb-07	Mar-07	Apr-07	Jun-07	Jul-07	Aug-07	Sep-07	Oct-07	Nov-07	Dec-07	Jan-08	Feb-08
Amphipoda																
Gammaridean	h															
Talitridae (4)		0.38 ± 0.71	0.00 ± 0.00	0.60 ± 0.96	0.10 ± 0.28	16.69 ± 10.26	1.32 ± 1.95	0.28 ± 0.68	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.14 ± 0.27	0.22 ± 0.48	0.29 ± 0.57
Stenothoidae (6)		0.15 ± 0.28	0.00 ± 0.00	0.44 ± 0.55	0.20 ± 0.37	4.69 ± 1.83	4.25 ± 8.75	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.28	0.21 ± 0.62	0.00 ± 0.00	2.21 ± 3.85	1.34 ± 1.21	2.48 ± 3.38
Podoceridae (3)		0.20 ± 0.38	0.00 ± 0.00	0.03 ± 0.08	0.10 ± 0.30	3.81 ± 2.44	3.20 ± 3.72	0.00 ± 0.00	0.52 ± 1.27	0.00 ± 0.00	0.20 ± 0.57	0.22 ± 0.52	0.00 ± 0.00	0.28 ± 0.39	1.29 ± 1.26	5.25 ± 2.55
Maxillipidae (4)		0.12 ± 0.34	0.00 ± 0.00	0.09 ± 0.28	0.00 ± 0.00	0.09 ± 0.20	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.07	0.00 ± 0.00	0.00 ± 0.00
Synopiidae (2)		0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.12	0.10 ± 0.28	1.74 ± 2.47	1.89 ± 4.50	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.21 ± 1.68	2.72 ± 3.97	13.07 ± 14.28
Dogielinotidae (1)		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Amphithoidae																
Amphitoe spp.	h	0.07 ± 0.20	0.00 ± 0.00	0.04 ± 0.13	0.00 ± 0.00	0.00 ± 0.00	1.76 ± 3.36	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.12 ± 0.33	0.24 ± 0.48	0.00 ± 0.00	0.10 ± 0.30	0.00 ± 0.00	3.24 ± 4.73
Dexaminidae (2)		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.92 ± 2.39	5.27 ± 5.72	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.22 ± 0.45	0.27 ± 0.69	0.38 ± 0.60	13.08 ± 12.40
Corophiidae (2)		±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
Corophium spp.	d	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Alicolor spp.		0.49 ± 1.38	0.00 ± 0.00	0.26 ± 0.56	0.86 ± 0.62	1.58 ± 2.19	1.04 ± 2.54	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.28	0.06 ± 0.18	0.00 ± 0.00	0.26 ± 0.39	1.99 ± 2.62	5.08 ± 10.33
Ampeliscidae (2)	d															
Byblis kallarthrus		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.13 ± 0.21
Ampelisca spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Melitidae (2)	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.17 ± 0.38	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.12 ± 0.23	0.04 ± 0.11	2.36 ± 2.89
Gammaridean Juvenile		8.95 ± 11.71	0.06 ± 0.15	11.12 ± 10.98	1.96 ± 1.79	91.32 ± 28.42	136.24 ± 56.24	2.79 ± 4.32	7.48 ± 4.95	4.24 ± 6.71	4.09 ± 4.84	2.80 ± 3.62	0.99 ± 1.25	13.58 ± 12.36	22.19 ± 13.67	182.95 ± 106.12
Caprellidean	h	0.15 ± 0.28	0.27 ± 0.57	0.50 ± 1.11	2.04 ± 2.61	111.77 ± 68.92	5.15 ± 7.33	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.20	0.00 ± 0.00	1.37 ± 1.69	12.66 ± 14.86	91.36 ± 73.53
Hyperidean																
Oxycephalidae	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.17 ± 0.38	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Polychaeta (44)	c, h, d	0.83 ± 1.06	0.37 ± 0.33	0.99 ± 1.25	0.59 ± 0.65	0.98 ± 0.79	1.46 ± 1.78	5.44 ± 5.88	1.30 ± 2.49	0.93 ± 1.02	0.99 ± 0.93	0.02 ± 0.07	0.66 ± 1.03	0.09 ± 0.17	0.82 ± 1.57	0.86 ± 1.23
Tubeworm	f															
Hydroides spp.		0.00 ± 0.00	0.16 ± 0.29	0.12 ± 0.37	0.06 ± 0.16	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.23 ± 0.41	0.00 ± 0.00	0.04 ± 0.13	0.33 ± 0.58	0.62 ± 1.11
Spirorbis spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Decapoda																
Brachyura																
Menaethius monoceros	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.09 ± 0.19	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Majidae juvenile	h	0.14 ± 0.41	0.12 ± 0.29	0.10 ± 0.31	0.00 ± 0.00	0.16 ± 0.22	2.18 ± 3.28	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.21 ± 0.62	0.13 ± 0.37	0.36 ± 0.82	0.00 ± 0.00
Xanthidae																
Liagore spp.	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Phymodius spp.	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Dynomene spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.77	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Lobster juvenile	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.41 ± 0.90	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Anomura																
Porcellanidae juvenile																
Liosoporcellana quadrilobata	vs, d	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Hermit crab	h, d	1.06 ± 1.24	0.30 ± 0.36	0.11 ± 0.25	0.19 ± 0.35	0.57 ± 0.71	2.78 ± 3.20	1.38 ± 2.21	2.70 ± 4.20	0.60 ± 1.10	0.96 ± 0.96	0.30 ± 0.41	1.00 ± 1.86	0.24 ± 0.38	0.08 ± 0.16	0.14 ± 0.29
Macrura																
Penaeid shrimp	c	0.46 ± 0.85	0.00 ± 0.00	0.29 ± 0.93	0.00 ± 0.00	0.07 ± 0.16	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.09 ± 0.25	0.00 ± 0.00	0.00 ± 0.00
Barnacle	f															
Chthamalus spp.		1.00 ± 1.36	0.96 ± 0.90	1.78 ± 1.43	11.03 ± 3.81	10.83 ± 3.65	81.10 ± 47.25	23.67 ± 20.46	20.04 ± 23.74	14.68 ± 27.86	1.94 ± 2.94	1.56 ± 1.92	0.27 ± 0.72	1.08 ± 1.06	2.95 ± 7.00	21.72 ± 22.86
Cirripedia larvae		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Copepoda																
Calanoida	f															
Temora turbinata		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Labidocera minuta		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Harpacticoida	d	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.15	0.20 ± 0.41	0.19 ± 0.23	5.22 ± 4.07	0.33 ± 0.68
Echinodermata																
Brittle star																
Ophiothrix spp.	vs, d	0.00 ± 0.00	0.00 ± 0.00	0.48 ± 1.39	0.00 ± 0.00	0.00 ± 0.00	0.56 ± 1.78	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.25	0.00 ± 0.00	0.26 ± 0.73	0.51 ± 0.81	1.03 ± 1.59
Sea urchin																
Salamacis dussumieri	h	0.00 ± 0.00	0.00 ± 0.00	0.06 ± 0.19	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.15 ± 0.37	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Anthocidaris crassispina	o	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.52 ± 1.27	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Temnopleurus hirsutimaculatus	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Starfish larvae		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Fish larva & juvenile																
Sebastiscus marmoratus	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Blennidae	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Pelates quadrilineatus	c	0.12 ± 0.34	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.12
Pranesticus breviceps	o	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.12

Table 4.3 (cont'd)

Taxonomic groups	Trophic mode	Nov-06	Dec-06	Jan-07	Feb-07	Mar-07	Apr-07	Jun-07	Jul-07	Aug-07	Sep-07	Oct-07	Nov-07	Dec-07	Jan-08	Feb-08
Mollusca																
Gastropoda																
Prosobranchia																
Pyrene scripta	d, h	0.48 ± 0.69	0.00 ± 0.00	0.55 ± 0.93	0.61 ± 0.83	0.69 ± 0.73	0.51 ± 1.14	3.40 ± 5.05	2.56 ± 2.31	1.52 ± 1.43	0.76 ± 0.88	0.23 ± 0.36	0.05 ± 0.16	0.52 ± 0.40	0.76 ± 0.98	1.27 ± 1.70
Pyrene spp	d, h	0.99 ± 0.96	0.29 ± 0.57	0.49 ± 0.92	0.10 ± 0.29	0.40 ± 0.39	7.59 ± 10.77	0.00 ± 0.00	0.41 ± 1.01	0.00 ± 0.00	0.10 ± 0.28	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.14	0.08 ± 0.23
Mitra spp.	d	0.59 ± 0.84	0.23 ± 0.29	0.19 ± 0.29	0.11 ± 0.20	0.68 ± 0.90	3.81 ± 6.01	2.37 ± 2.73	3.93 ± 6.73	2.62 ± 5.45	0.13 ± 0.23	0.33 ± 0.46	0.80 ± 0.83	0.36 ± 0.63	0.53 ± 0.79	0.81 ± 1.08
Mitra rugosum	d, c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.77	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Tectarius sp.1		0.43 ± 0.70	0.65 ± 1.43	0.11 ± 0.28	0.20 ± 0.57	0.33 ± 0.35	51.75 ± 31.96	6.15 ± 13.48	0.68 ± 1.08	0.30 ± 0.72	4.87 ± 11.10	0.39 ± 0.69	0.00 ± 0.00	0.04 ± 0.13	1.81 ± 4.86	1.94 ± 3.07
Tectarius sp.2		0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.31	0.15 ± 0.30	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Marginella spp.	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cancellaria spp.	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Lunella coronata		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.06 ± 0.16	0.13 ± 0.30	0.24 ± 0.77	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Lunella spp. juvenile		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cerithidea spp.	h	0.29 ± 0.43	0.12 ± 0.30	0.09 ± 0.29	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.12	0.24 ± 0.47	0.05 ± 0.14	0.03 ± 0.09	0.00 ± 0.00
Monodonta neritoides	h	0.10 ± 0.29	0.04 ± 0.09	0.00 ± 0.00	0.00 ± 0.00	0.09 ± 0.19	0.46 ± 0.99	0.68 ± 1.07	1.18 ± 1.37	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.23
Astraea rhodostigma	h	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.06	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.36 ± 0.89	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Littorina spp.	h	0.12 ± 0.34	0.20 ± 0.50	0.00 ± 0.00	0.00 ± 0.00	0.26 ± 0.59	0.79 ± 2.50	1.79 ± 2.61	0.00 ± 0.00	0.30 ± 0.74	0.39 ± 1.11	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Morula spp.		0.12 ± 0.34	0.00 ± 0.00	0.06 ± 0.19	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.54 ± 1.33	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Oliva spp.	sv, c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Tectus conus		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.06 ± 0.18
Tectus pyramis	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.30	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cronia margaritícola		0.15 ± 0.41	0.00 ± 0.00	0.00 ± 0.00	0.20 ± 0.37	0.26 ± 0.58	0.52 ± 1.11	0.00 ± 0.00	0.00 ± 0.00	0.15 ± 0.36	0.00 ± 0.00	0.14 ± 0.35	0.00 ± 0.00	0.20 ± 0.39	0.00 ± 0.00	0.14 ± 0.30
Turritella spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Crepidula spp.	f	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cantharus spp.		0.07 ± 0.20	0.00 ± 0.00	0.10 ± 0.31	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.77	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.25	0.00 ± 0.00	0.04 ± 0.11	0.00 ± 0.00
Epitonium spp.		0.19 ± 0.37	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.25 ± 0.79	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.27 ± 0.76	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.06 ± 0.19
Thais luteostoma		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.54 ± 1.33	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Notoacmoea Schrenkii		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Diodora ticaonica	f	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Balcis spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cypraea gracilis	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Cypraea arabicus	h	0.00 ± 0.00	0.12 ± 0.29	0.00 ± 0.00	0.00 ± 0.00	0.17 ± 0.38	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.25	0.13 ± 0.37	0.00 ± 0.00	0.00 ± 0.00
Telescopium spp. juvenile		0.07 ± 0.20	0.12 ± 0.29	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Gastropoda juvenile	f	0.00 ± 0.00	0.00 ± 0.00	0.30 ± 0.61	0.40 ± 0.62	2.19 ± 2.25	0.36 ± 1.14	1.66 ± 2.80	0.73 ± 1.79	0.00 ± 0.00	0.00 ± 0.00	0.82 ± 0.78	0.11 ± 0.32	0.28 ± 0.31	0.00 ± 0.00	0.31 ± 0.92
Nudibranchia																
Aplysia juliana	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Chromodoris pallescens	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Bivalvia	f															
Ostrea cucullata		0.12 ± 0.34	0.29 ± 0.57	0.18 ± 0.57	0.10 ± 0.28	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.41 ± 1.01	0.94 ± 1.04	0.00 ± 0.00	0.05 ± 0.14	0.23 ± 0.62	0.00 ± 0.00	0.00 ± 0.00	0.15 ± 0.46
Isognomon spp.		0.08 ± 0.23	0.00 ± 0.00	0.09 ± 0.29	0.00 ± 0.00	0.07 ± 0.16	0.00 ± 0.00	0.00 ± 0.00	0.41 ± 1.01	0.36 ± 0.89	0.33 ± 0.75	0.15 ± 0.33	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.25	0.00 ± 0.00
Siliqua spp.		0.00 ± 0.00	0.04 ± 0.09	0.09 ± 0.29	0.19 ± 0.36	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.07 ± 0.20	0.00 ± 0.00	0.17 ± 0.50
Cardita leana		0.24 ± 0.69	0.08 ± 0.19	0.24 ± 0.48	0.20 ± 0.37	0.09 ± 0.19	0.58 ± 1.24	1.79 ± 3.35	0.26 ± 0.64	0.00 ± 0.00	0.15 ± 0.29	0.20 ± 0.31	0.08 ± 0.25	0.22 ± 0.63	0.35 ± 0.74	0.10 ± 0.29
Pteria spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Pinctada spp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Spondylus sinensis		0.00 ± 0.00	0.04 ± 0.09	0.09 ± 0.29	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.28 ± 0.66	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.13	0.00 ± 0.00	0.00 ± 0.00
Barbatia obliqua		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.28 ± 0.89	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.15	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Barbatia sp.		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.09 ± 0.18	1.96 ± 2.90	1.00 ± 1.37	0.03 ± 0.09	5.22 ± 8.06
Barbatia spp. juvenile		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Septifer bilocularis		0.12 ± 0.34	0.12 ± 0.29	0.00 ± 0.00	0.19 ± 0.36	0.66 ± 0.73	0.28 ± 0.89	0.49 ± 1.20	1.14 ± 1.87	0.85 ± 1.68	0.33 ± 0.75	0.16 ± 0.34	0.08 ± 0.25	0.05 ± 0.15	0.16 ± 0.49	0.82 ± 1.99
Septifer virgatus		1.05 ± 1.21	0.18 ± 0.29	0.39 ± 0.51	0.20 ± 0.29	0.65 ± 0.82	1.03 ± 1.39	5.71 ± 7.61	0.00 ± 0.00	0.19 ± 0.47	0.90 ± 0.71	0.30 ± 0.39	0.08 ± 0.25	0.20 ± 0.44	0.57 ± 0.97	0.15 ± 0.46
Chama reflexa		1.89 ± 1.22	0.65 ± 0.86	1.48 ± 1.71	1.31 ± 1.39	0.51 ± 0.49	1.49 ± 1.59	8.36 ± 9.58	1.51 ± 1.88	0.66 ± 1.03	0.71 ± 1.80	0.63 ± 0.55	0.44 ± 1.08	0.10 ± 0.18	0.07 ± 0.14	0.27 ± 0.55
Placamen calophylla		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.15	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mytilidae sp.1 juvenile		0.15 ± 0.41	0.00 ± 0.00	0.32 ± 0.92	0.31 ± 0.63	1.00 ± 1.41	0.58 ± 1.24	0.00 ± 0.00	0.52 ± 1.27	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.10	0.58 ± 1.63	0.65 ± 1.04
Mytilidae sp.2 juvenile		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.69 ± 2.20	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Nuculidae		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mysidacea																
Lophogaster pacificus	c	0.00 ± 0.00	0.06 ± 0.15	0.33 ± 0.69	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.19 ± 0.47	0.91 ± 0.97	0.09 ± 0.18	0.00 ± 0.00	0.26 ± 0.29	0.39 ± 0.81	0.80 ± 1.62
Sirella vulgaris	o	0.16 ± 0.45	0.00 ± 0.00	0.04 ± 0.13	0.00 ± 0.00	0.00 ± 0.00	1.08 ± 3.42	0.00 ± 0.00	0.82 ± 2.02	0.00 ± 0.00	0.45 ± 0.77	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.03 ± 0.09	0.00 ± 0.00
Unidentified mysis	o	0.19 ± 0.37	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Mysidae juvenile	o	0.57 ± 1.36	0.12 ± 0.29	0.12 ± 0.29	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.73 ± 1.79	0.00 ± 0.00	0.00 ± 0.00	0.28 ± 0.46	0.00 ± 0.00	0.07 ± 0.20	0.17 ± 0.50	0.06 ± 0.18
Cnidaria																
Hydroid polyp	c	0.00 ± 0.00	0.10 ± 0.25	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	1.18 ± 1.95
Isopoda	h	1.31 ± 1.72	0.06 ± 0.15	1.73 ± 2.78	0.96 ± 1.60	2.49 ± 2.18	14.98 ± 10.17	1.75 ± 3.54	10.94 ± 9.95	1.64 ± 3.22	3.14 ± 3.50	1.57 ± 2.09	1.53 ± 1.61	1.52 ± 1.51	1.34 ± 1.65	4.15 ± 4.01
Chiton	h	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.13	0.00 ± 0.00	0.00 ± 0.00
Sea Anemone	c	0.00 ± 0.00	0.00 ± 0.00	0.13 ± 0.30	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.03 ± 0.08	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Stomatopoda, Mantis shrimp	c	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Sipuncula, Peanut worm	d	0.00 ± 0.00	0.16 ± 0.29	0.38 ± 0.94	0.33 ± 0.76	0.09 ± 0.19	0.79 ± 1.35	2.78 ± 2.90	0.26 ± 0.64	0.15 ± 0.36	0.22 ± 0.41	0.00 ± 0.00	0.17 ± 0.50	0.18 ± 0.30	0.35 ± 0.82	0.10 ± 0.29
Sponge	f	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.07 ± 0.16	0.25 ± 0.79	0.00 ± 0.00	0.62 ± 1.51	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.12	0.33 ± 0.68	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.29
Others, e.g. insecta		0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.11 ± 0.32	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Total		25.61 ± 17.58	5.90 ± 5.90	24.68 ± 18.13	23.03 ± 9.30	257.67 ± 70.28	337.67 ± 70.50	71.85 ± 35.43	59.66 ± 26.87	30.83 ± 25.70	22.16 ± 23.81	11.65 ± 7.22	7.90 ± 4.73	26.08 ± 21.43	60.26 ± 32.77	357.52 ± 183.43

Table 4.4 Results of Pairwise ANOSIM comparisons among **(A)** sampling months and **(B)** growth stages of *Sargassum siliquastrum* (values in bold indicate $p<0.05$) and SIMPER analysis showing the discriminating taxa between groups in LLT. Discriminating taxa are those making a large contribution to differences between growth stages, listed in order of decreasing importance.

(A)

Pairwise ANOSIM												
	Nov-06	Dec-06	Jan-07	Feb-07	Mar-07	May-07	Jun-07	Aug-07	Sep-07	Oct-07	Nov-07	Dec-07
Dec-06	0.23	\										
Jan-07	0.457	0.024	\									
Feb-07	0.565	0.25	0.354	\								
Mar-07	0.303	0.186	0.452	0.318	\							
May-07	0.222	0.26	0.628	0.609	0.476	\						
Jun-07	0.153	0.319	0.64	0.759	0.613	0.523	\					
Aug-07	0.208	0.264	0.463	0.48	0.129	0.165	-0.022	\				
Sep-07	0.171	0.054	0.107	0.324	0.163	0.047	0.236	0.162	\			
Oct-07	0.115	0.25	0.299	0.464	0.249	0.235	0.306	0.31	0.04	\		
Nov-07	0.488	0.408	0.442	0.512	0.279	0.511	0.701	0.457	0.229	-0.02	\	
Dec-07	0.617	0.426	0.557	0.482	0.306	0.758	0.816	0.588	0.438	0.359	0.243	\
Feb-08	0.633	0.604	0.86	0.737	0.543	0.784	0.81	0.573	0.519	0.549	0.582	0.367
SIMPER												
	Nov-06	Dec-06	Jan-07	Feb-07	Mar-07	May-07	Jun-07	Aug-07	Sep-07	Oct-07	Nov-07	Dec-07
Dec-06	H	\										
Jan-07	H, G1, B	n.s.	\									
Feb-07	n.s.	n.s.	n.s.	\								
Mar-07	n.s.	n.s.	H	n.s.	\							
May-07	G23	H	H, B	n.s.	n.s.	\						
Jun-07	BS, GJ, B	H, BS, GJ	H, BS, GJ	BS, C, GJ	BS, GJ	BS, GJ, B	\					
Aug-07	GJ	H, GJ	H, GJ	GJ	GJ	GJ	B, BS	\				
Sep-07	BS, B	n.s.	n.s.	n.s.	n.s.	B	GJ, BS	GJ	\			
Oct-07	G1, B, TH	H	H	n.s.	n.s.	B, G23	BS, GJ, G3	GJ	BS	\		
Nov-07	G1, B, TH	TH, H	H, TH	n.s.	TH	B, TH	BS, GJ, TH	GJ, TH	TH	TH	\	
Dec-07	GL	n.s.	GL	n.s.	n.s.	n.s.	GJ, BS	GJ	GL	GL	TH	\
Feb-08	n.s.	n.s.	H	n.s.	n.s.	n.s.	GJ, BS	GJ	n.s.	n.s.	TH	n.s.

(B)

Pairwise ANOSIM						
	06-Rapid Growth	06-Reproductive	07-Dieback	07-Slow Growth	07-Rapid Growth	07-Reproductive
06-Reproductive	0.462	\				
07-Dieback	0.565	0.156	\			
07-Slow Growth	0.052	0.138	-0.053	\		
07-Rapid Growth	0.32	0.167	0.159	0.155	\	
07-Reproductive	0.617	0.307	0.482	-0.036	0.005	\
08-Dieback	0.633	0.565	0.737	-0.034	0.202	0.367
SIMPER						
	06-Rapid Growth	06-Reproductive	07-Dieback	07-Slow Growth	07-Rapid Growth	07-Reproductive
06-Reproductive	n.s.	\				
07-Dieback	n.s.	n.s.	\			
07-Slow Growth	BS	H	n.s.	\		
07-Rapid Growth	B, G1	H	n.s.	n.s.	\	
07-Reproductive	GL	n.s.	n.s.	n.s.	GL	\
08-Dieback	n.s.	H	n.s.	GJ	n.s.	n.s.

Taxa abbreviations: B= Barnacle of *Chthamalus* spp., BS= Brittle star of *Ophiothrix* spp., C= Caprellidean, G1= Gastropod *Pyrene scripta*, G3= Gastropod *Tectarius* spp., G23= Gastropod *Cantharus* spp., GJ= Gammaridean juvenile, GL= Gastropod larvae, H= Harpacticoid, TH= Tubeworm *Hydroides* spp, n.s.= no significant result.

Table 4.5 Results of Pairwise ANOSIM comparisons among **(A)** sampling months and **(B)** growth stages of *Sargassum siliquastrum* (values in bold indicate $p<0.05$) and SIMPER analysis showing the discriminating taxa between groups in LLS. Discriminating taxa are those making a large contribution to differences between growth stages, listed in order of decreasing importance.

(A)

Pairwise ANOSIM										
	Nov-06	Dec-06	Jan-07	Feb-07	Apr-07	May-07	Jun-07	Oct-07	Nov-07	Dec-07
Dec-06	0.127	\								
Jan-07	0.019	-0.123	\							
Feb-07	0.158	0.3	0.055	\						
Apr-07	0.065	0.072	-0.104	0.078	\					
May-07	0.131	0	-0.164	0.15	0.108	\				
Jun-07	0.393	0.1	0.119	0.631	0.637	0.523	\			
Oct-07	0.117	0.058	0.036	0.292	0.255	0.261	0.54	\		
Nov-07	0.357	0.266	0.248	0.241	0.405	0.427	0.679	0.089	\	
Dec-07	0.594	0.562	0.366	0.373	0.462	0.646	0.974	0.401	0.283	\
Feb-08	0.601	0.574	0.34	0.333	0.527	0.646	0.896	0.517	0.398	0.168
SIMPER										
	Nov-06	Dec-06	Jan-07	Feb-07	Apr-07	May-07	Jun-07	Oct-07	Nov-07	Dec-07
Dec-06	n.s.	\								
Jan-07	G1	B, G1	\							
Feb-07	GJ	GJ	GJ	\						
Apr-07	HC, C	C	C	C, G20	\					
May-07	GJ, B	GJ, B	B, GJ	B	C, B	\				
Jun-07	n.s.	B	G1	GJ	GJ, C	GJ	\			
Oct-07	n.s.	n.s.	B	n.s.	n.s.	n.s.	GJ	\		
Nov-07	n.s.	GJ	B, G1	G5	G20, C	B, G5	GJ, B	n.s.	\	
Dec-07	GJ	GJ, C	GJ, B, C	n.s.	n.s.	B	GJ, B	n.s.	C	\
Feb-08	GJ	GJ, C	GJ, C, B	n.s.	G20	B	GJ, B, C	n.s.	C	n.s.

(B)

Pairwise ANOSIM						
	06-Rapid Growth	06-Reproductive	07-Dieback	07-Slow Growth	07-Rapid Growth	07-Reproductive
06-Reproductive	0.026	\				
07-Dieback	0.158	0.056	\			
07-Slow Growth	0.154	-0.002	0.118	\		
07-Rapid Growth	0.355	0.188	0.291	0.246	\	
07-Reproductive	0.594	0.195	0.373	0.223	0.157	\
08-Dieback	0.601	0.224	0.333	0.279	0.302	0.168
SIMPER						
	06-Rapid Growth	06-Reproductive	07-Dieback	07-Slow Growth	07-Rapid Growth	07-Reproductive
06-Reproductive	n.s.	\				
07-Dieback	GJ	GJ	\			
07-Slow Growth	n.s.	n.s.	GJ	\		
07-Rapid Growth	n.s.	n.s.	n.s.	B	\	
07-Reproductive	GJ	GJ, C	n.s.	GJ, B	n.s.	\
08-Dieback	GJ	GJ, C	n.s.	GJ, B	C	n.s.

Taxa abbreviations: B= Barnacle of *Chthamalus* spp., C= Caprellidean, G1= Gastropod *Pyrene scripta*, G5= Gastropod *Pyrene* spp., G20= Gastropod *Cronia margariticola*, GJ= Gammaridean juvenile, HC= Hermit crab, n.s.= no significant result.

Table 4.6 Results of Pairwise ANOSIM comparisons among **(A)** sampling months and **(B)** growth stages of *Sargassum siliquastrum* (values in bold indicate $p<0.05$) and SIMPER analysis showing the discriminating taxa between groups in LFN. Discriminating taxa are those making a large contribution to differences between growth stages, listed in order of decreasing importance.

(A)

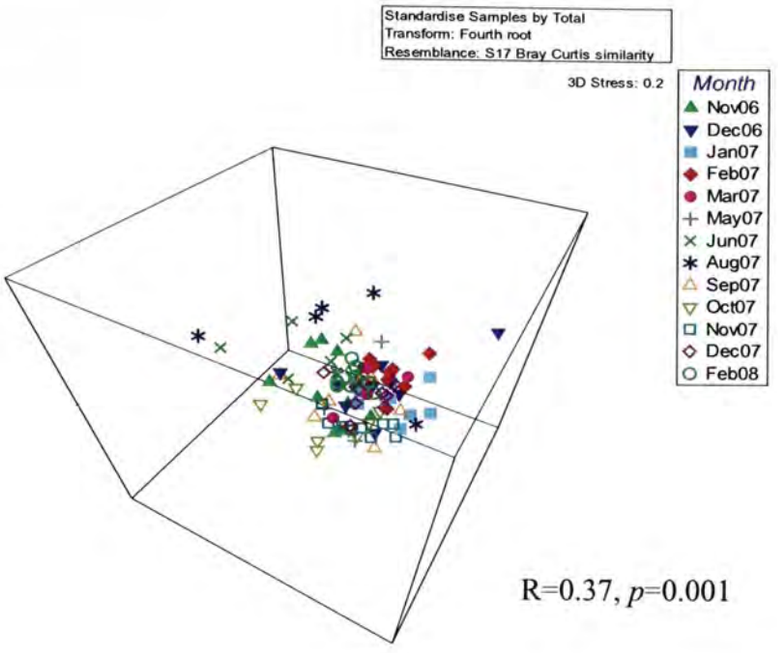
Pairwise ANOSIM														
	Nov-06	Dec-06	Jan-07	Feb-07	Mar-07	Apr-07	Jun-07	Jul-07	Aug-07	Sep-07	Oct-07	Nov-07	Dec-07	Jan-08
Dec-06	0.106	\												
Jan-07	0.03	0.393	\											
Feb-07	0.347	0.407	0.191	\										
Mar-07	0.42	0.408	0.187	0.541	\									
Apr-07	0.471	0.613	0.372	0.645	0.557	\								
Jun-07	0.117	0.046	0.329	0.395	0.827	0.794	\							
Jul-07	0.141	0.256	0.24	0.276	0.704	0.628	0.278	\						
Aug-07	0.196	0.059	0.403	0.391	0.328	0.659	0.133	-0.052	\					
Sep-07	0.139	0.398	0.243	0.531	0.608	0.504	0.369	0.164	0.205	\				
Oct-07	0.08	0.202	0.111	0.217	0.377	0.502	0.218	0.082	0.166	0.1	\			
Nov-07	0.197	0.171	0.362	0.478	0.366	0.543	0.364	0.006	0.06	0.161	0.128	\		
Dec-07	0.534	0.617	0.228	0.426	0.397	0.584	0.784	0.614	0.483	0.49	0.32	0.395	\	
Jan-08	0.71	0.725	0.497	0.648	0.607	0.761	0.919	0.834	0.671	0.7	0.574	0.532	0.193	\
Feb-08	0.709	0.738	0.532	0.752	0.814	0.704	0.952	0.856	0.667	0.753	0.648	0.568	0.546	0.58
SIMPER														
	Nov-06	Dec-06	Jan-07	Feb-07	Mar-07	Apr-07	Jun-07	Jul-07	Aug-07	Sep-07	Oct-07	Nov-07	Dec-07	Jan-08
Dec-06	GJ	\												
Jan-07	GJ	GJ	\											
Feb-07	B, GJ, HC	B, GJ, HC	B	\										
Mar-07	C	GJ, C	C	C, B	\									
Apr-07	G3, CR, GJ	GJ, G3	G3	G3, GJ	C, G3	\								
Jun-07	GJ, HC	CR, HC, B	GJ	GJ, GA, C	C, GJ	GJ, G3, CR	\							
Jul-07	I, GJ, CR	I, GJ, B	I, B	I, B, GA	C	G3, G1, B	I, CR, GJ	\						
Aug-07	B, CR, GJ	B, G1, GJ	GJ, B, CR	B, GJ, GA	C, GJ, B	B, G3, GJ	B, CR, GJ	I, B, GJ	\					
Sep-07	CR, GJ, B	GJ, I, B	CR, G3	B, G3, I	C	B, LP	B, I, CR	B, SV, G3	I, GJ, B	\				
Oct-07	GL, GJ, B	GJ, GL, I	B	B, GJ, GL	C	G3, B, GL	B, GJ, I	B, GL, GJ	B, GJ, GL	GL, B, G3	\			
Nov-07	CR, B, GJ	I, GJ, B	I, CR, GJ	B, I, GJ	C	G3, B, GJ	B, CR, I	B, G1, GJ	I, GJ, G1	G3, SV, HC	GL, GJ, B	\		
Dec-07	CR, GJ	GJ	CR	B, GJ	C	G3	GJ, CR, C	C, B, GJ	GJ, C, B	C, G3	GJ	C, GJ	\	
Jan-08	H, C, CR	GJ, H, C	H, C, CR	B, H	H	H, B, G3	GJ, H, C	H, C, B	H, C, GJ	H, C	H, C, GL	C, H, I	H	\
Feb-08	C, CR, GJ	GJ, C	C, GG, CR	GG, GJ, B	GS, GT	C, G3, GS	C, GJ, CR	C, GG	C, GJ, B	C, GG	C, GG	C, GJ, B	GSt, GG	H, GSt

(B)

Pairwise ANOSIM						
	06-Rapid Growth	06-Reproductive	07-Dieback	07-Slow Growth	07-Rapid Growth	07-Reproductive
06-Reproductive	-0.13	\				
07-Dieback	0.347	-0.023	\			
07-Slow Growth	0.064	0.13	-0.019	\		
07-Rapid Growth	0.042	0.129	0.156	0.126	\	
07-Reproductive	0.788	0.417	0.599	0.176	0.328	\
08-Dieback	0.709	0.234	0.752	0.038	0.285	0.278
SIMPER						
	06-Rapid Growth	06-Reproductive	07-Dieback	07-Slow Growth	07-Rapid Growth	07-Reproductive
06-Reproductive	GJ	\				
07-Dieback	B, GJ, HC	B, GJ	\			
07-Slow Growth	GJ, CR	GJ	C, GJ	\		
07-Rapid Growth	GJ, CR, B	I, GJ, B	B, I	B, GJ, I	\	
07-Reproductive	CR, C, GJ	n.s.	B, H, GJ	C, B, H	C	\
08-Dieback	C, CR, GJ	C, GG	GG, GJ, B	C	C, GG	GSt, H

Taxa abbreviations: B= Barnacle of *Chthamalus* spp., C= Caprellidean, CR= *Chama reflexa*, G1= Gastropod *Pyrene scripta*, G3= Gastropod *Tectarius* spp., GA= Gammaridean *Aloiloi* spp., GG= Gammaridean *Guernea* spp., GS= Gammaridean of family Synopiidae, GSt= Gammaridean of family Stenothoidae, GT= Gammaridean of family Talitridae, GJ= Gammaridean juvenile, GL= Gastropod larvae, H= Harpacticoid, HC= Hermit crab, I= Isopoda, LP= *Lophogaster pacificus*, SV= *Septifier viridis*.

(A)



R=0.37, p=0.001

(B)

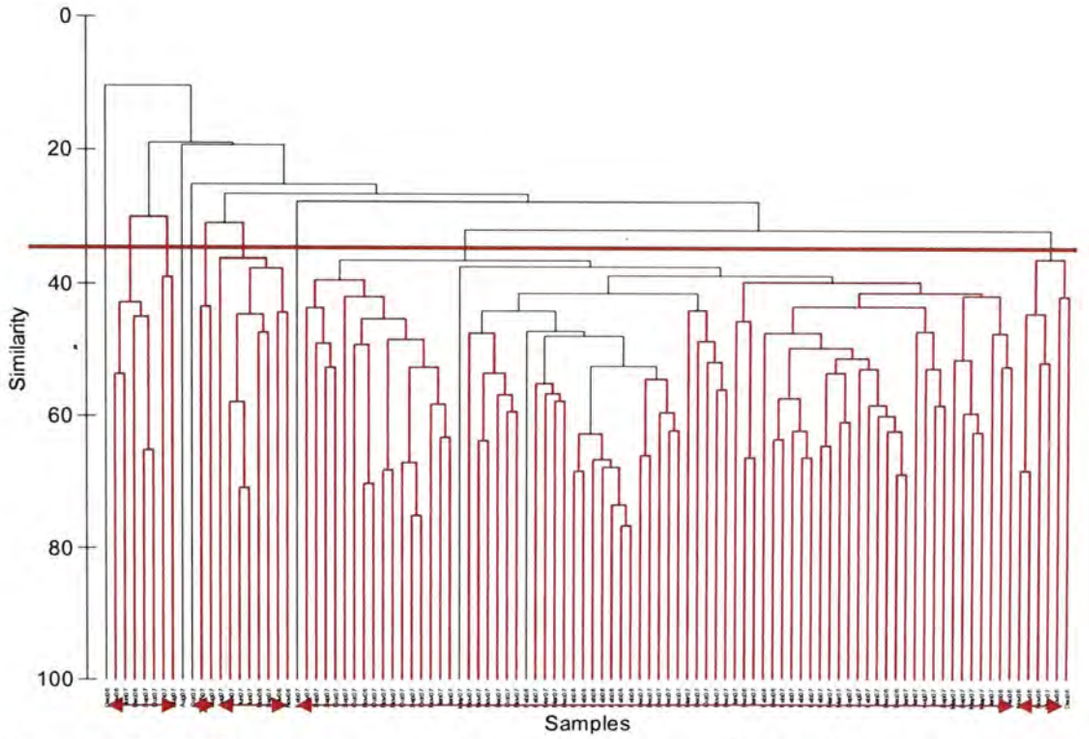
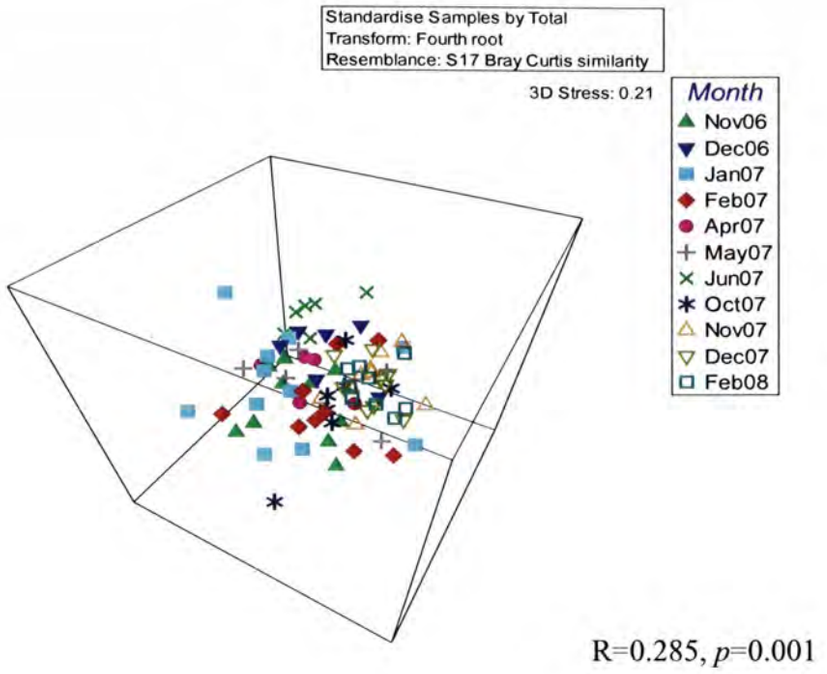


Fig. 4.1 **(A)** MDS ordination plot (stress = 0.2) and **(B)** Dendrogram based on Bray-Curtis similarity, fourth root transformed group average data showing the epiphytic faunal assemblages among sampling months in LLT. Each point represents data from each individual seaweed. ANOSIM results (with Global-R = 0.37) indicate significant overlapping in the faunal structure among months. Solid lines in dendrogram display groupings which are statistically significant (Simprof test, p<0.05).

(A)



R=0.285, p=0.001

(B)

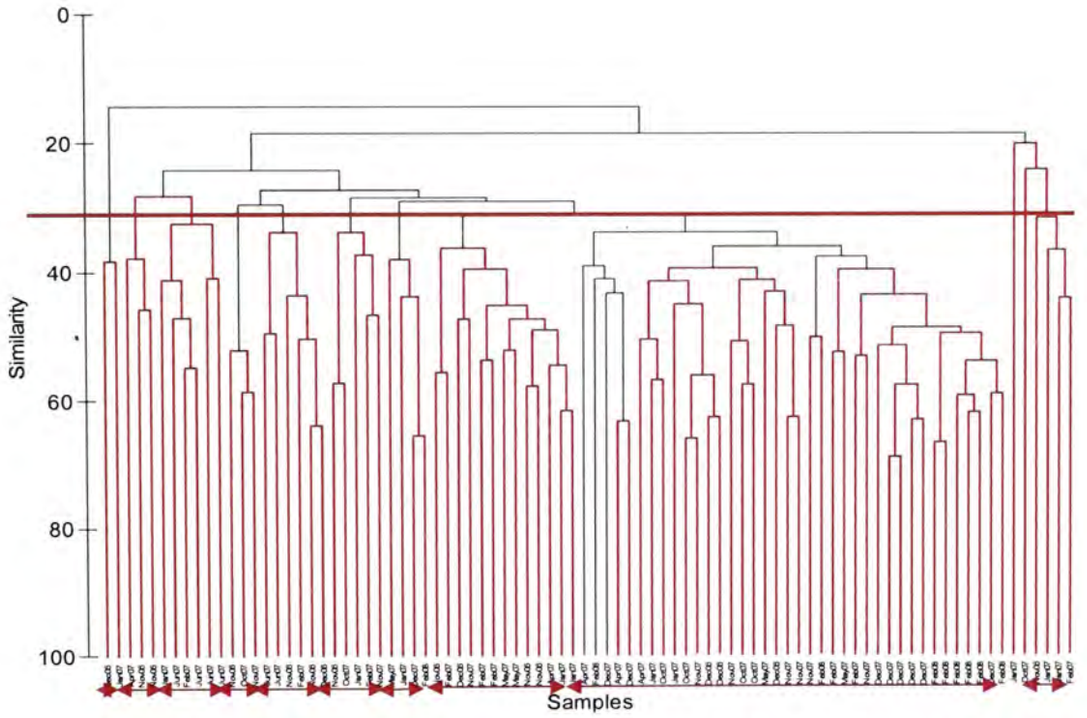
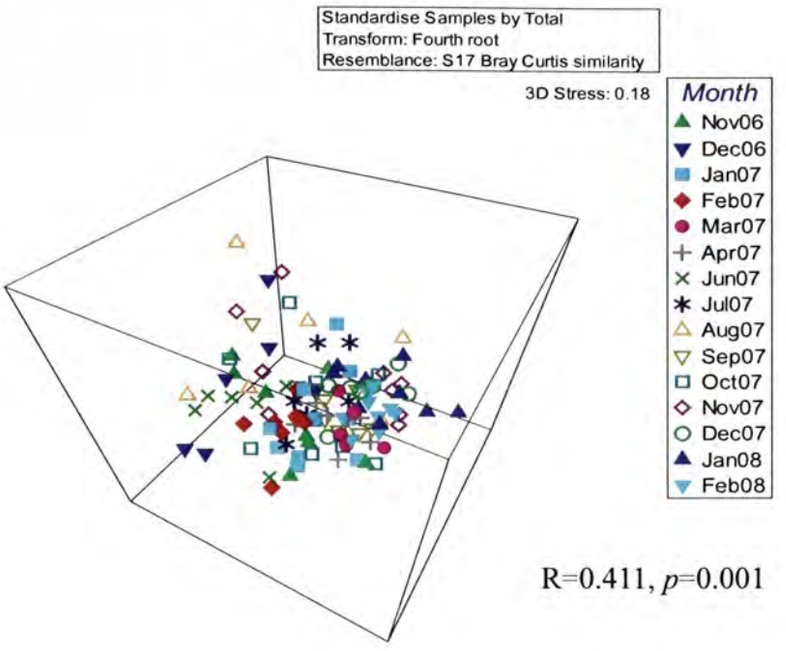


Fig. 4.2 **(A)** MDS ordination plot (stress = 0.21) and **(B)** Dendrogram based on Bray-Curtis similarity, fourth root transformed group average data showing the epiphytic faunal assemblages among sampling months in LLS. Each point represents data from each individual seaweed. ANOSIM results (with Global-R = 0.285) indicate significant overlapping in the faunal structure among months. Solid lines in dendrogram display groupings which are statistically significant (Simprof test, p<0.05).

(A)



(B)

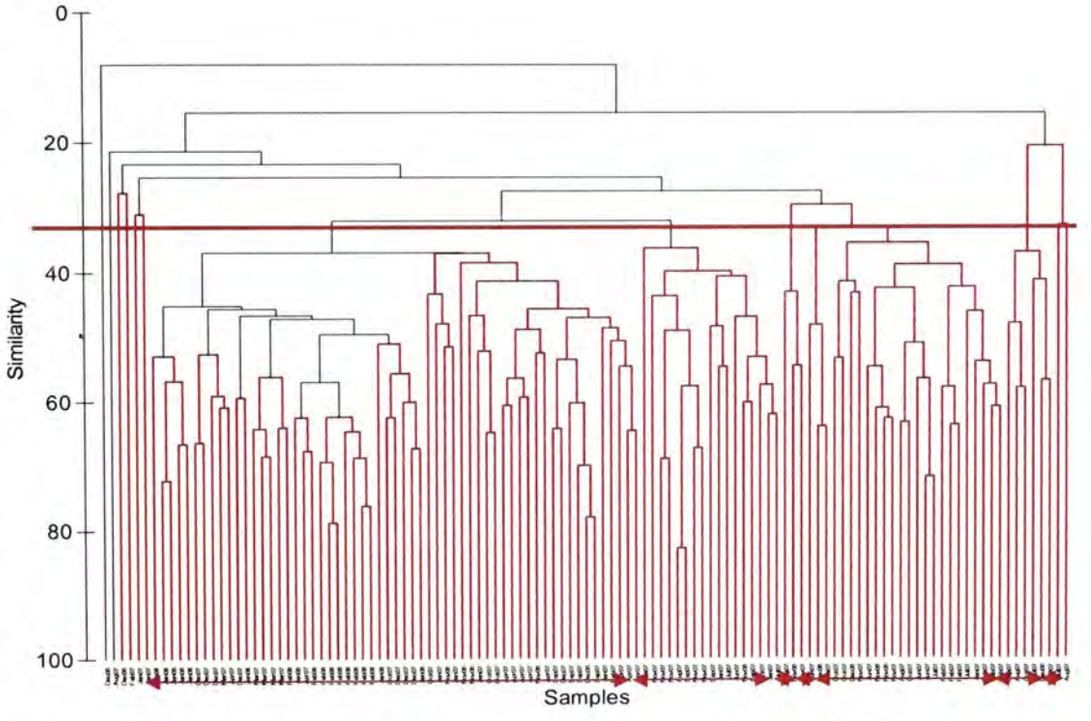
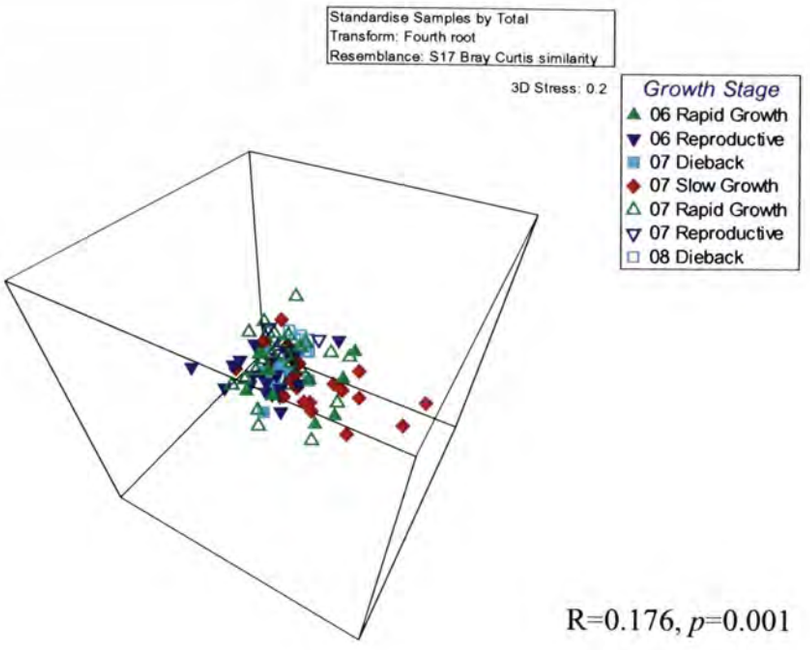


Fig. 4.3 **(A)** MDS ordination plot (stress = 0.18) and **(B)** Dendrogram based on Bray-Curtis similarity, fourth root transformed group average data showing the epiphytic faunal assemblages among sampling months in LFN. Each point represents data from each individual seaweed. ANOSIM results (with Global-R = 0.411) indicate significant overlapping in the faunal structure among months. Solid lines in dendrogram display groupings which are statistically significant (Simprof test, $p<0.05$).

(A)



R=0.176, p=0.001

(B)

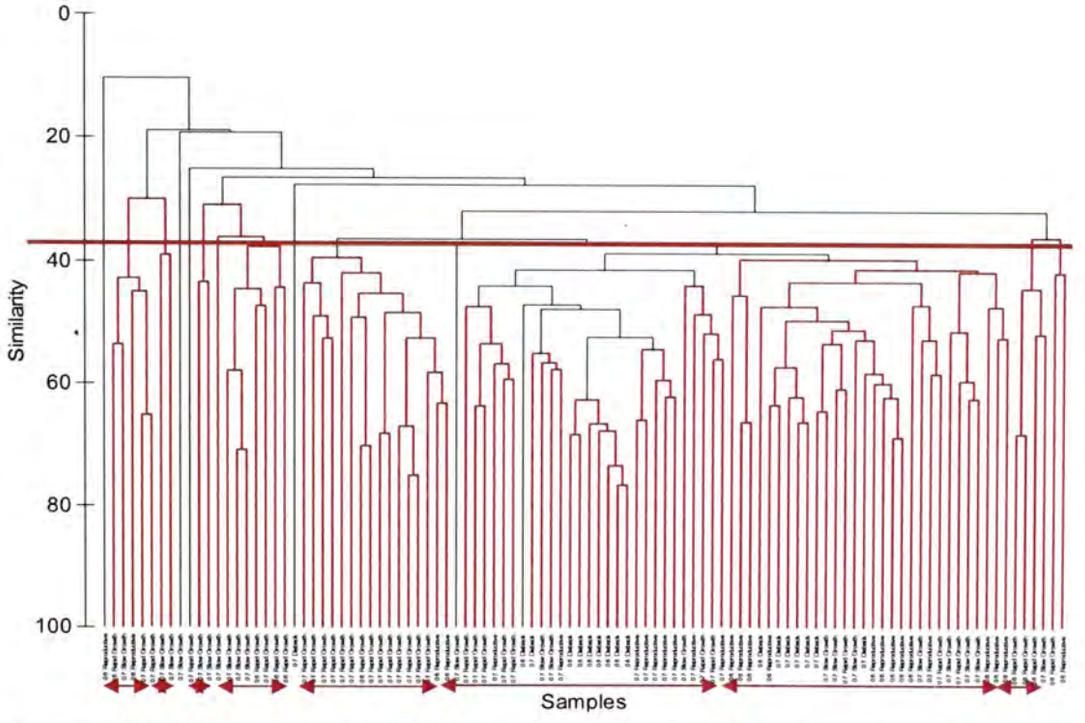
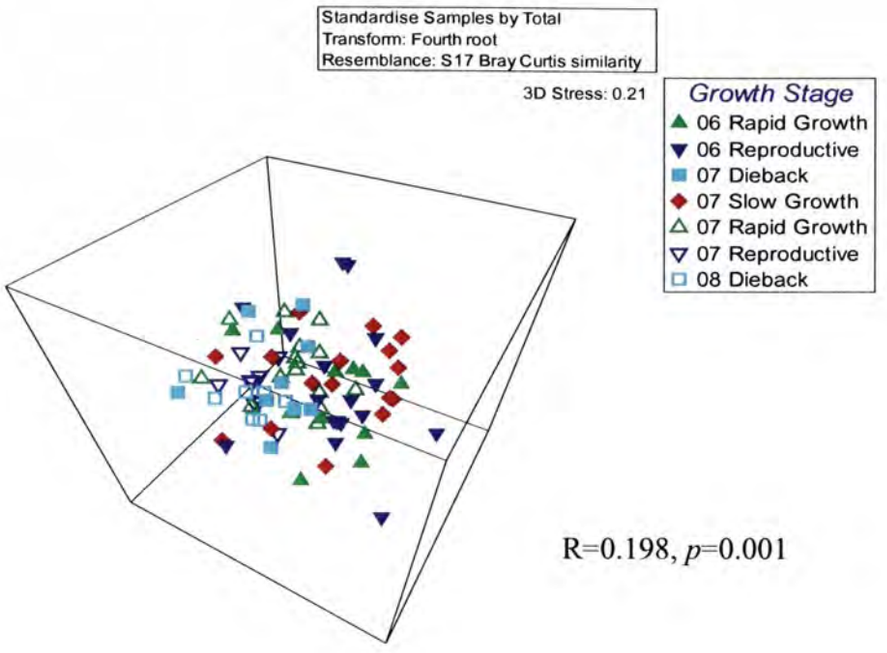


Fig. 4.4 **(A)** MDS ordination plot (stress = 0.2) and **(B)** Dendrogram based on Bray-Curtis similarity, fourth root transformed group average data showing the epiphytic faunal assemblages among seaweed growth stages in LLT. Each point represents data from each individual seaweed. ANOSIM results (with Global-R = 0.176) indicate significant overlapping in the faunal structure among stages. Solid lines in dendrogram display groupings which are statistically significant (Simprof test, p<0.05).

(A)



R=0.198, p=0.001

(B)

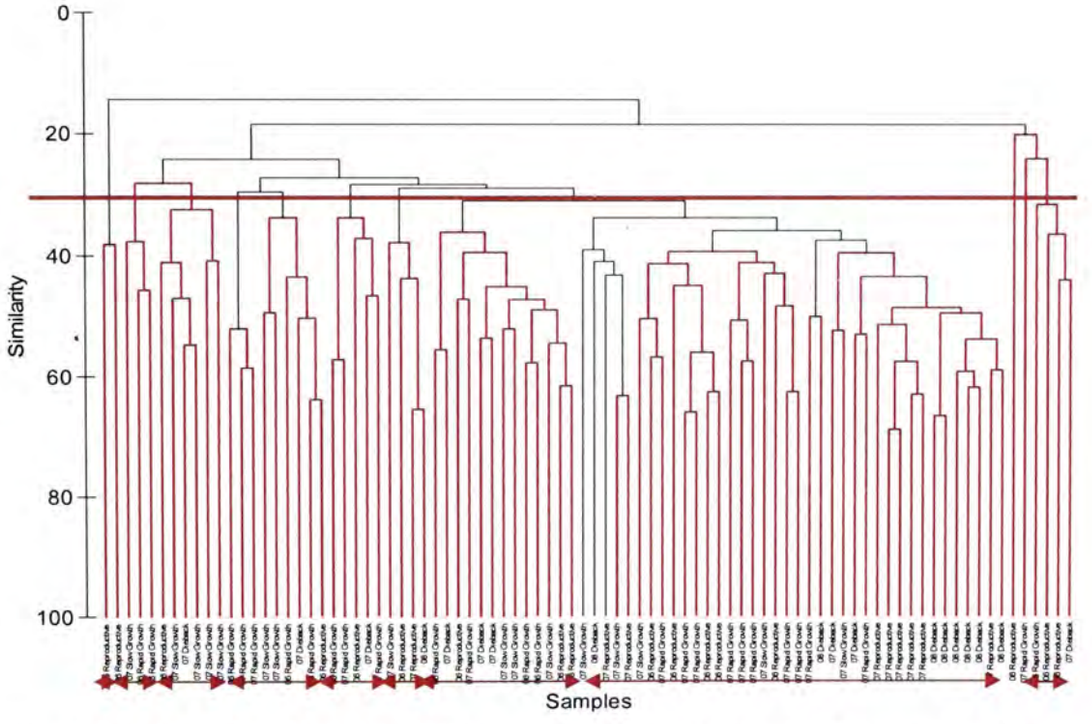
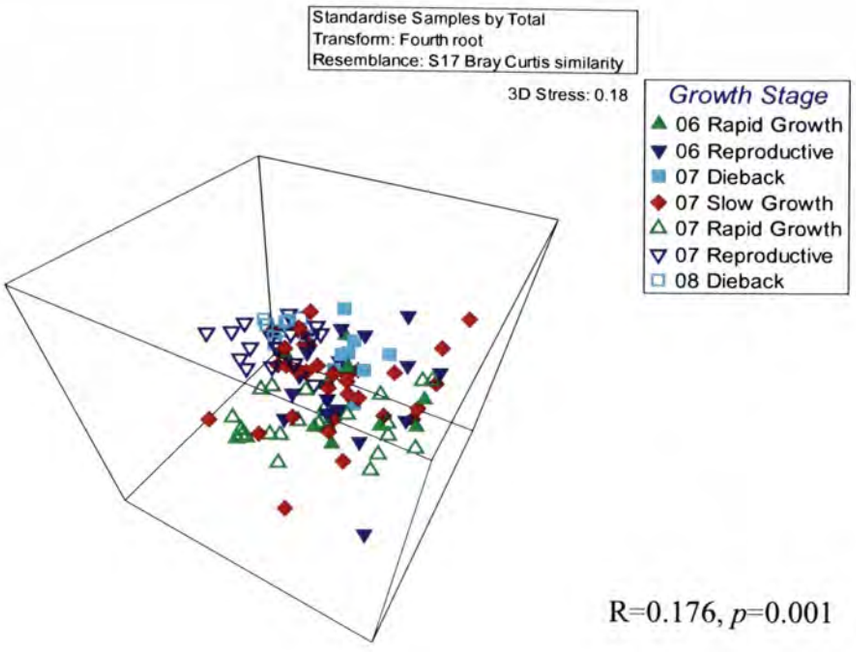


Fig. 4.5 **(A)** MDS ordination plot (stress = 0.21) and **(B)** Dendrogram based on Bray-Curtis similarity, fourth root transformed group average data showing the epiphytic faunal assemblages among seaweed growth stages in LLS. Each point represents data from each individual seaweed. ANOSIM results (with Global-R = 0.198) indicate significant overlapping in the faunal structure among stages. Solid lines in dendrogram display groupings which are statistically significant (Simprof test, p<0.05).

(A)



R=0.176, p=0.001

(B)

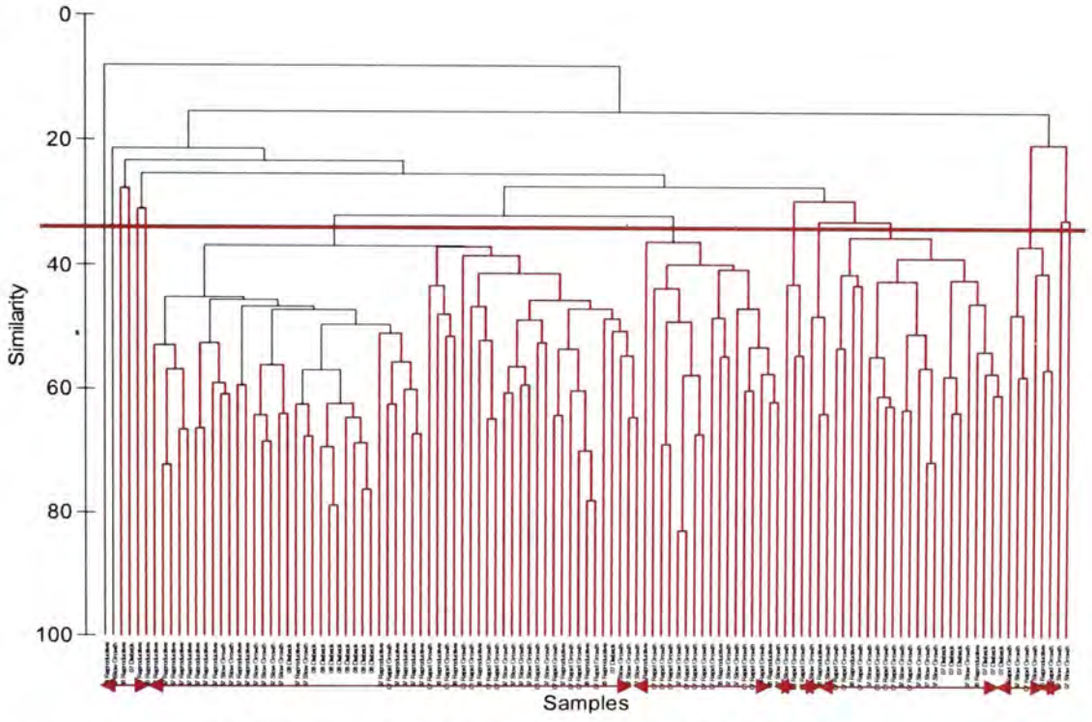
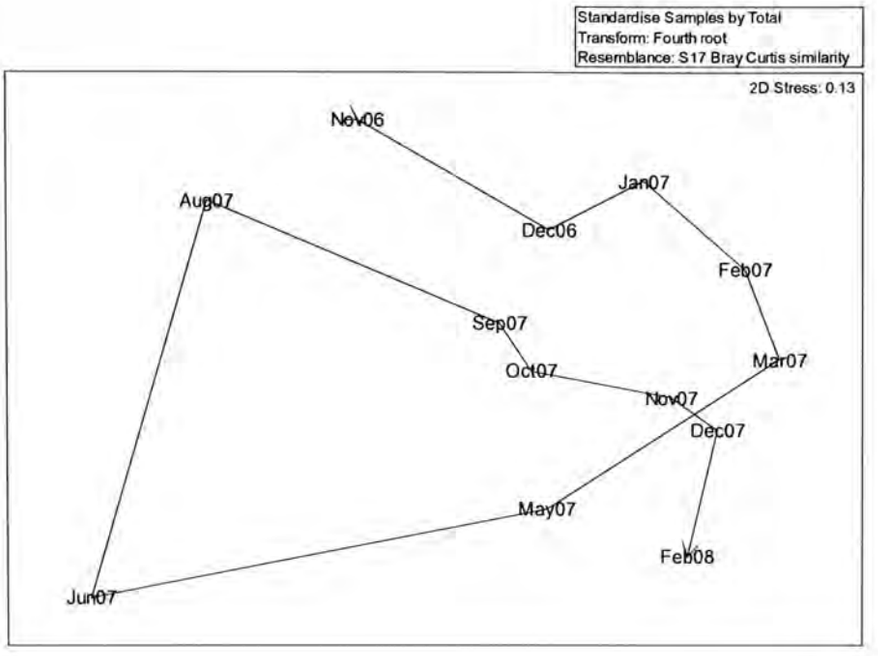


Fig. 4.6 **(A)** MDS ordination plot (stress = 0.18) and **(B)** Dendrogram based on Bray-Curtis similarity, fourth root transformed group average data showing the epiphytic faunal assemblages among seaweed growth stages in LFN. Each point represents data from each individual seaweed. ANOSIM results (with Global-R = 0.176) indicate significant overlapping in the faunal structure among stages. Solid lines in dendrogram display groupings which are statistically significant (Simprof test, p<0.05).

(A)



(B)

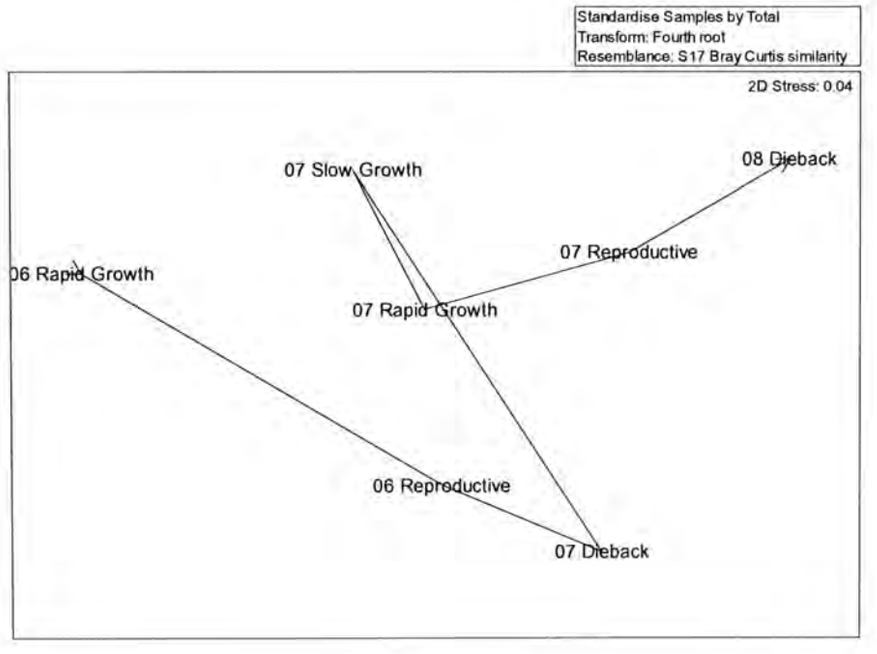
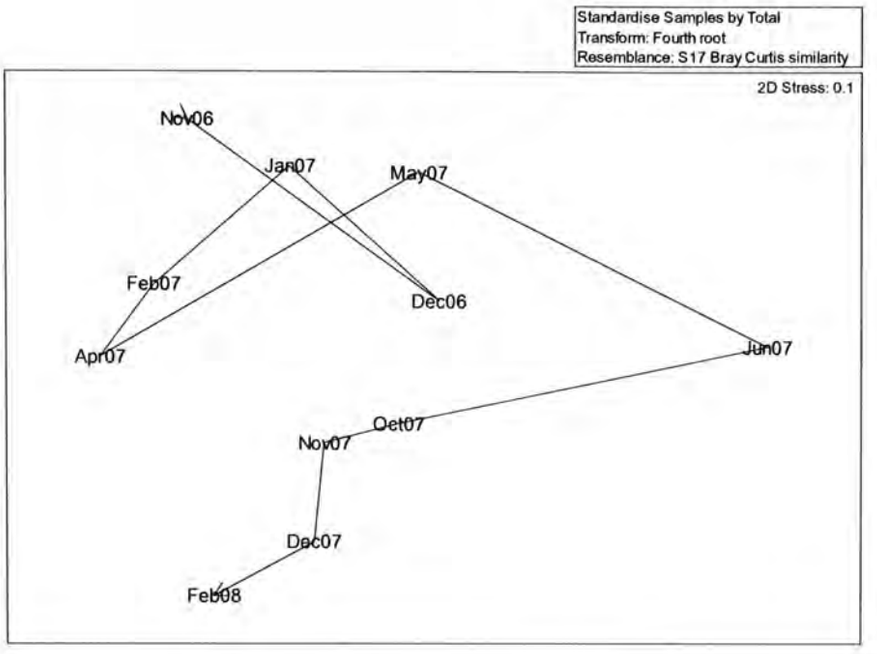


Fig. 4.7 MDS ordination plot showing the temporal shift in the structure of epiphytic faunal assemblages among **(A)** sampling months and **(B)** seaweed growth stages in LLT. Each point represents mean data from each individual seaweed.

(A)



(B)

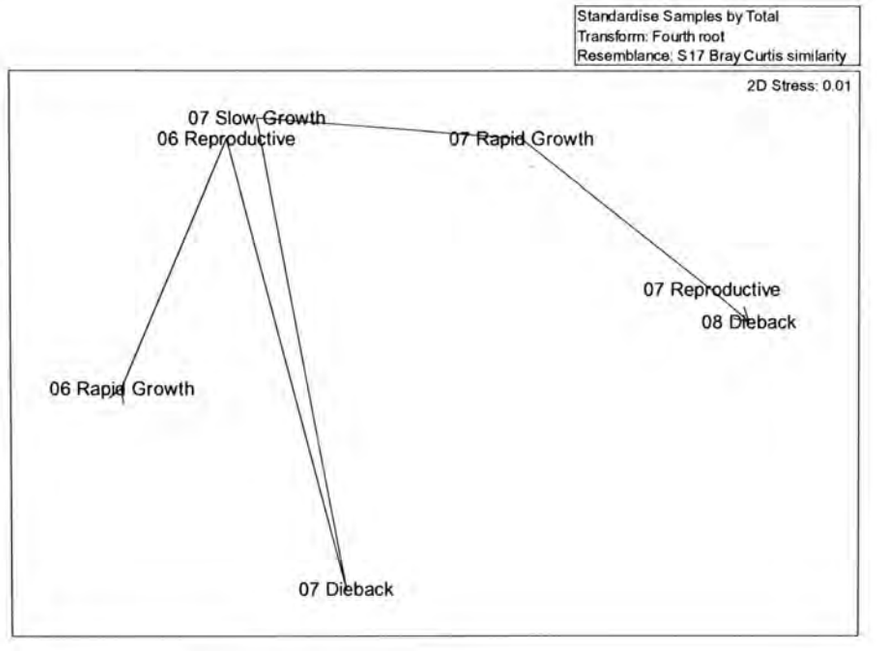
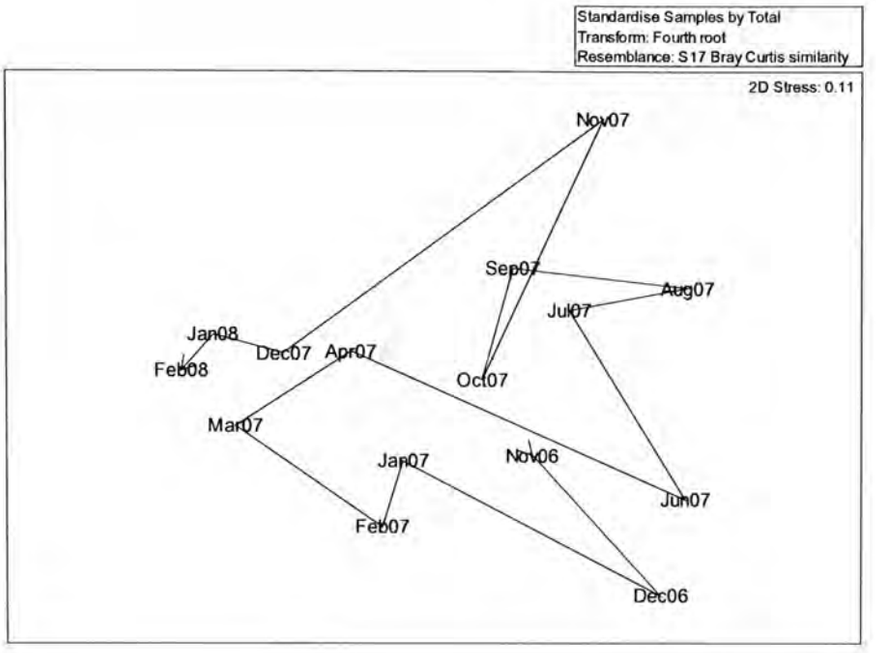


Fig. 4.8 MDS ordination plot showing the temporal shift in the structure of epiphytic faunal assemblages among **(A)** sampling months and **(B)** seaweed growth stages in LLS. Each point represents mean data from each individual seaweed.

(A)



(B)

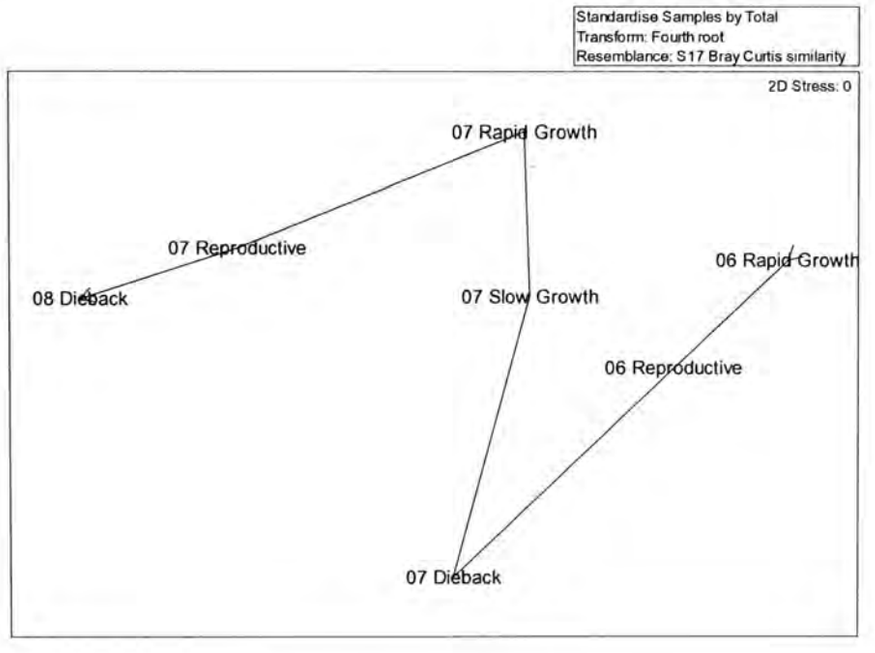


Fig. 4.9 MDS ordination plot showing the temporal shift in the structure of epiphytic faunal assemblages among **(A)** sampling months and **(B)** seaweed growth stages in LFN. Each point represents mean data from each individual seaweed.

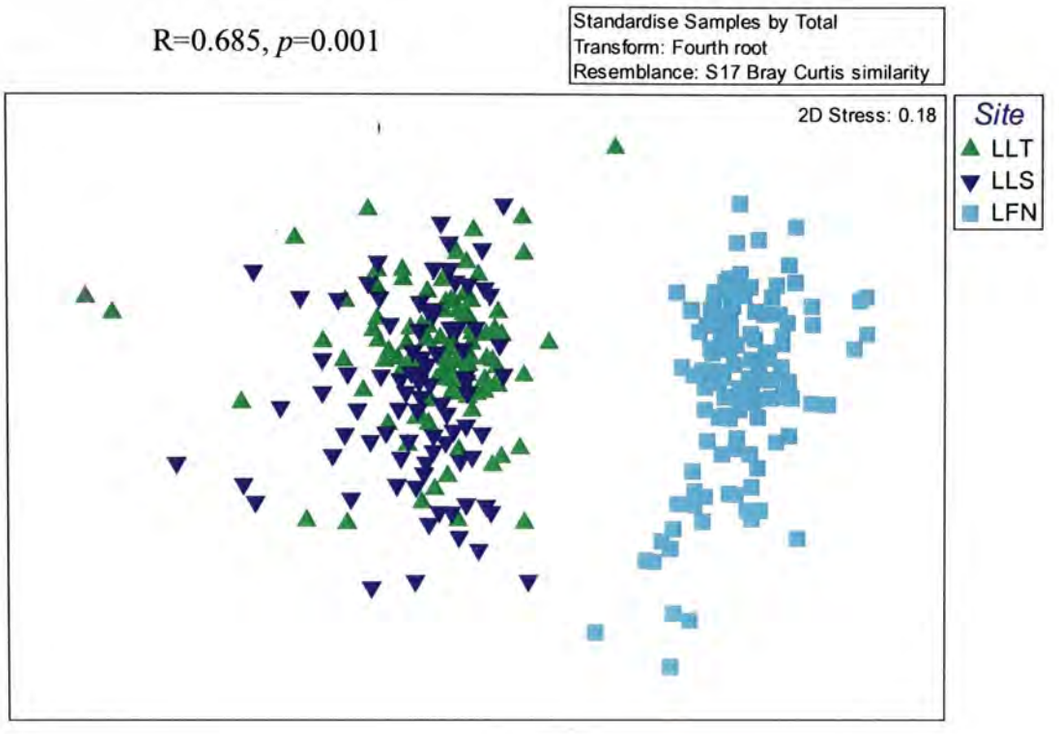


Fig. 4.10 MDS ordination plot showing the epiphytic faunal assemblages among different sites. Each point represents data from each individual seaweed. ANOSIM results (with Global-R = 0.685) show significant separation in the structure of epiphytic faunal assemblages among sites.

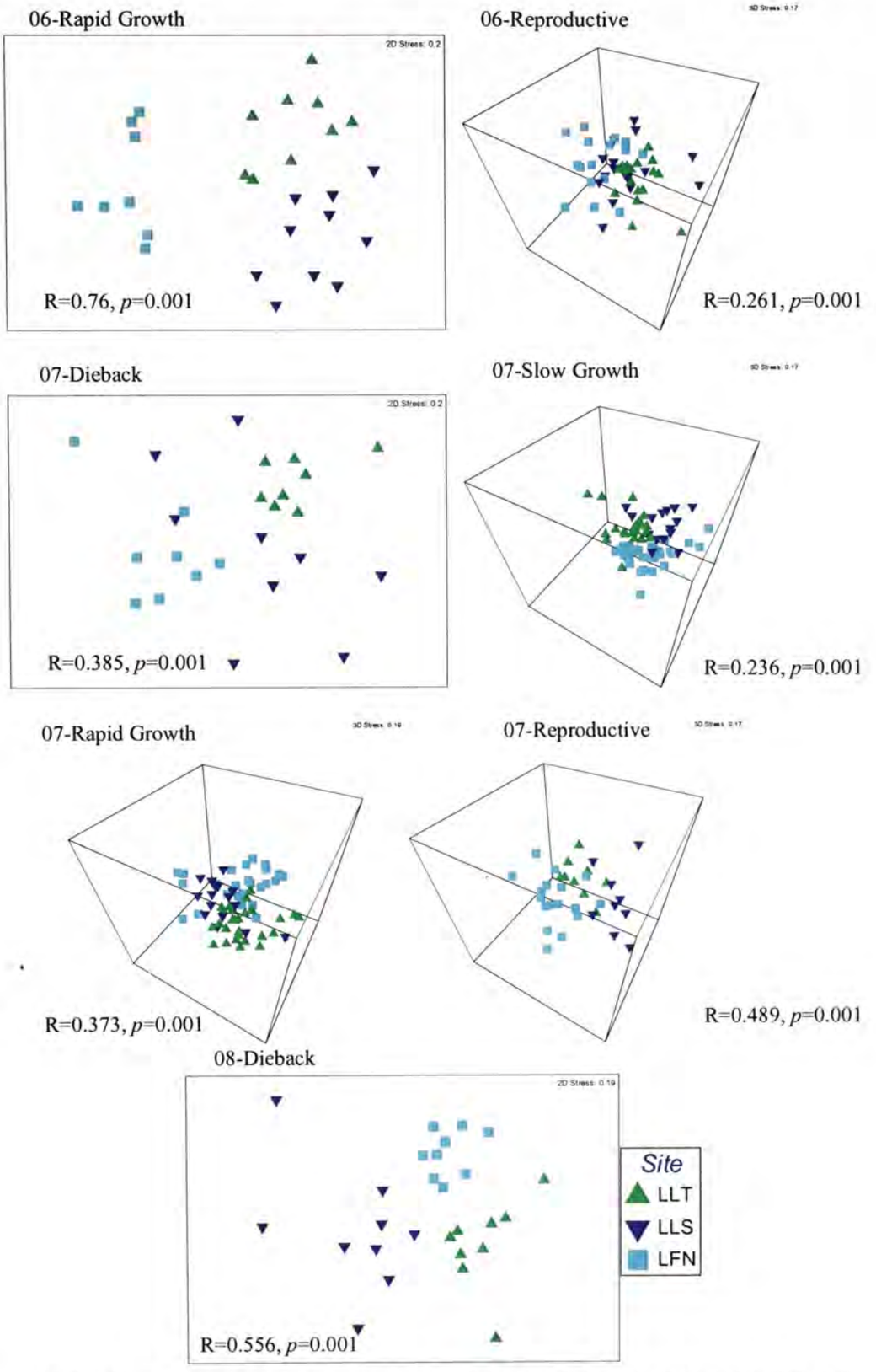


Fig. 4.11 MDS ordination plots based on Bray-Curtis similarities showing the epiphytic faunal assemblages among different sites in each seaweed growth stage. ANOSIM results indicate significant distinct separation in the structure of epiphytic faunal assemblages among sites in 06 Rapid Growth and 08 Dieback stages but not in other stages.

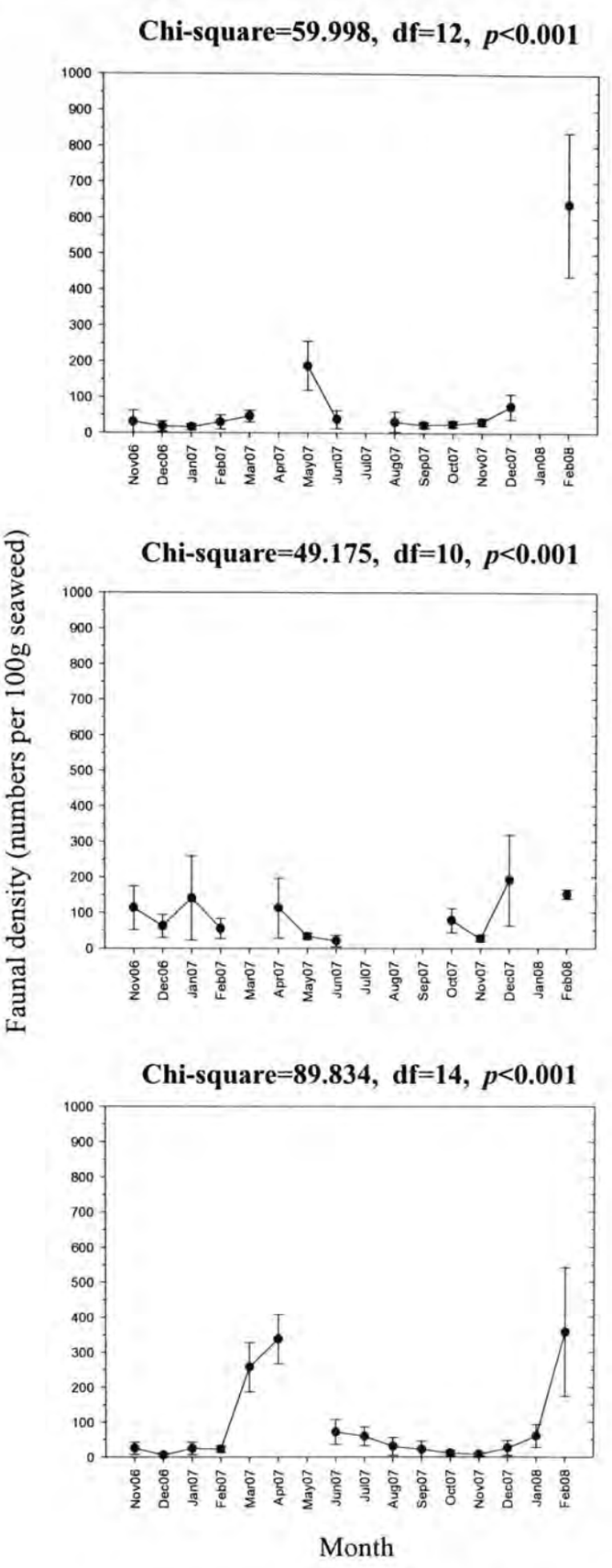
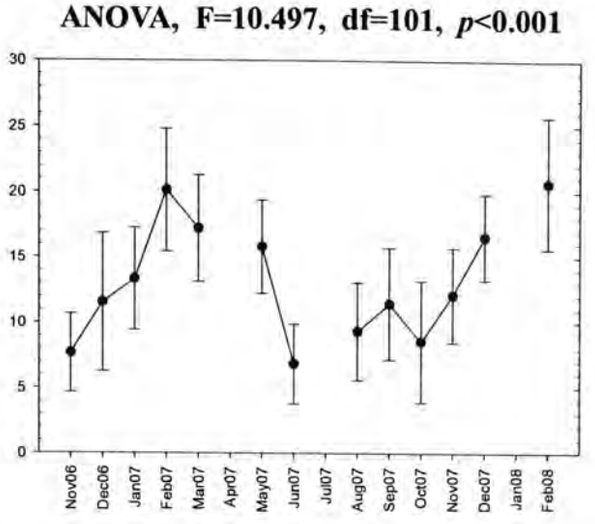
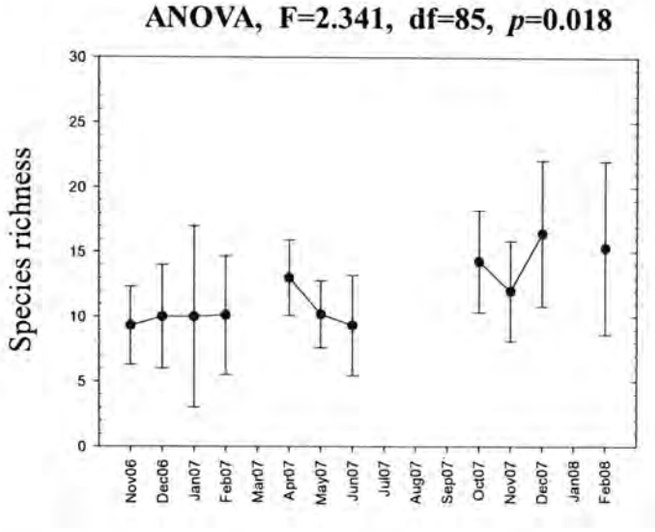


Fig. 4.12 Temporal change in mean (± S.D.) epiphytic faunal density in **(A)** LLT, **(B)** LLS and **(C)** LFN. Kruskal Wallis test results show significant differences in mean faunal density among months in each of the three sites. Missing data indicate no samplings taken in the respective months.

(A) LLT



(B) LLS



(C) LFN

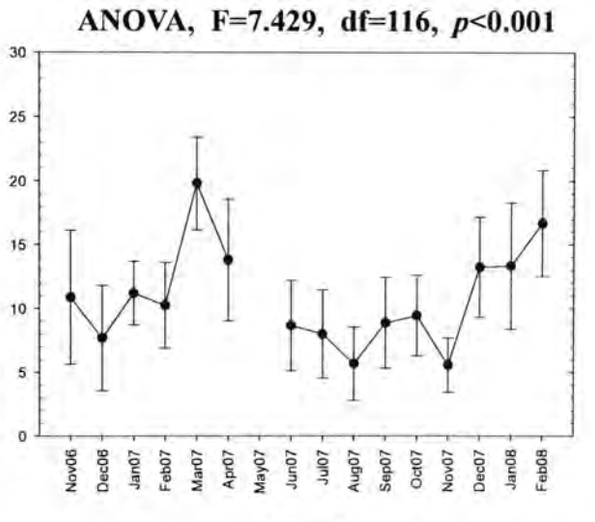


Fig. 4.13 Temporal change in mean (± S.D.) epiphytic faunal species richness in **(A)** LLT, **(B)** LLS and **(C)** LFN. One-way ANOVA results show significant differences in species richness among months in each of the three sites. Missing data indicate no samplings taken in the respective months.

(A) LLT

H': **ANOVA, F=2.260, df=101, p=0.015**

J: **Chi-square=59.674, df=12, p<0.001**

(B) LLS

H': **ANOVA, F=2.268, df=85, p=0.022**

J: **Chi-square=48.259, df=10, p<0.001**

(C) LFN

H': **ANOVA, F=2.671, df=116, p=0.002**

J: **Chi-square=77.570, df=14, p<0.001**

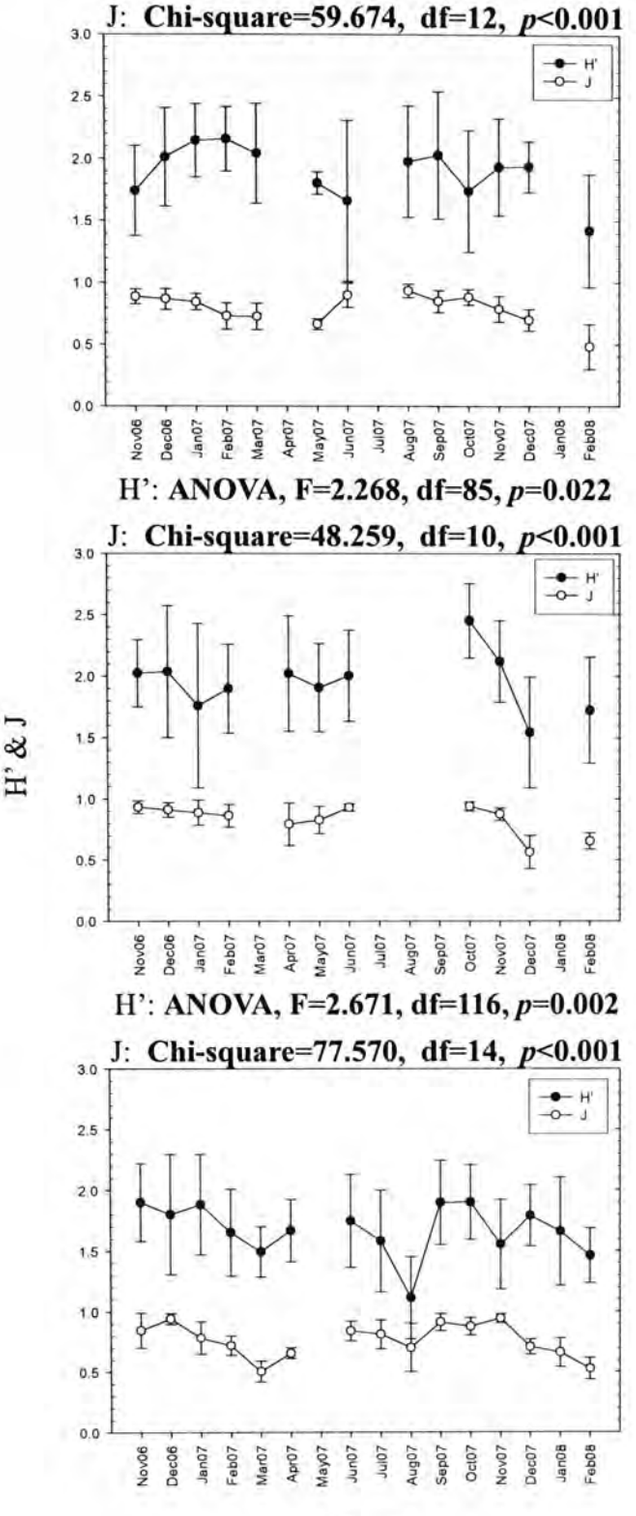


Fig. 4.14 Temporal change in mean (± S.D.) epiphytic faunal Shannon Diversity (H') and Evenness (J) Indices in **(A)** LLT, **(B)** LLS and **(C)** LFN. One-way ANOVA and Kruskal Wallis test results show significant differences in H' and J among months in each of the three sites. Missing data indicate no samplings taken in the respective months.

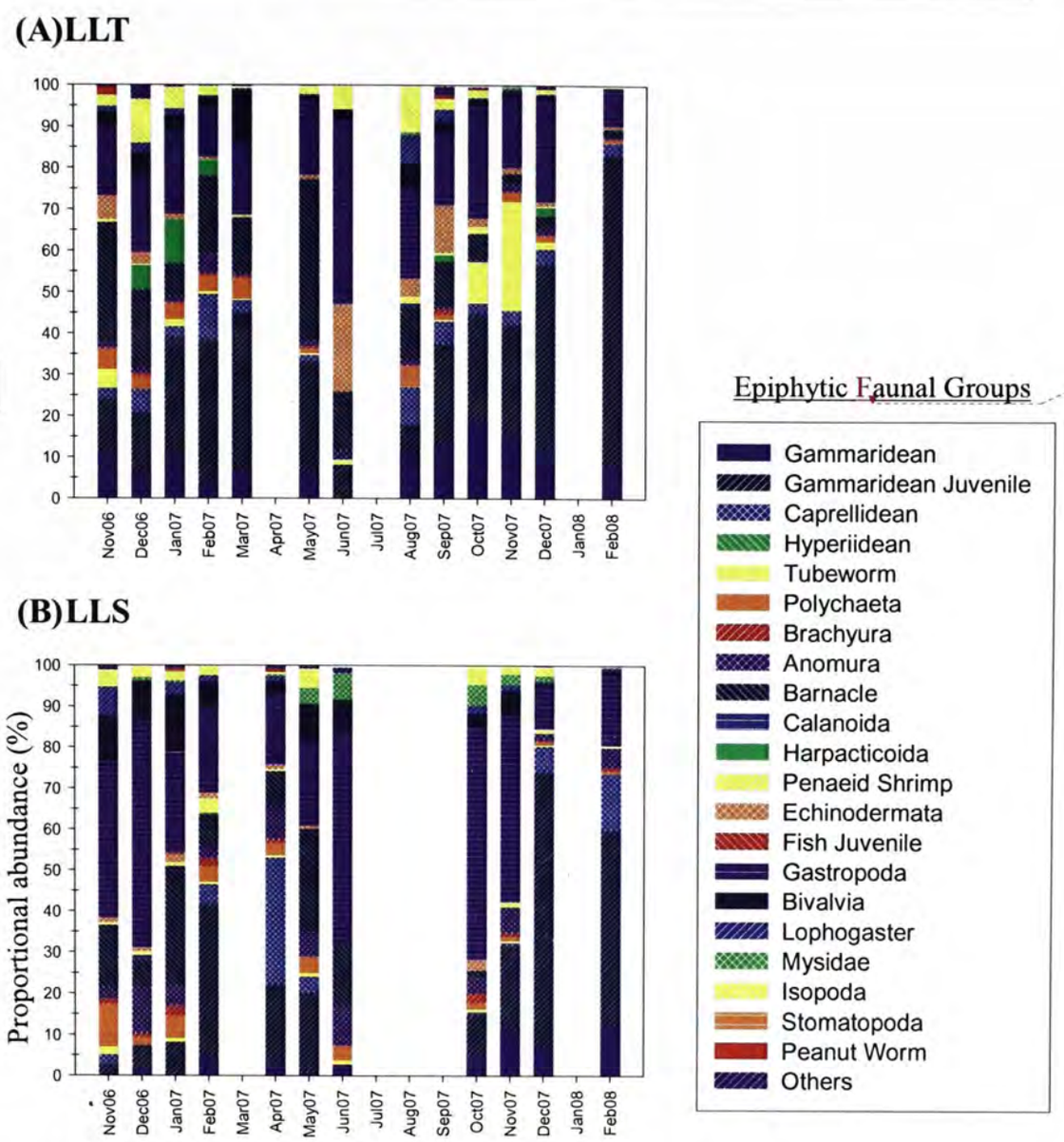


Fig. 4.15 Proportional abundance of epiphytic faunal groups in **(A)** LLT, **(B)** LLS and **(C)** LFN in each sampling month. Missing data indicate no samplings taken in those months.

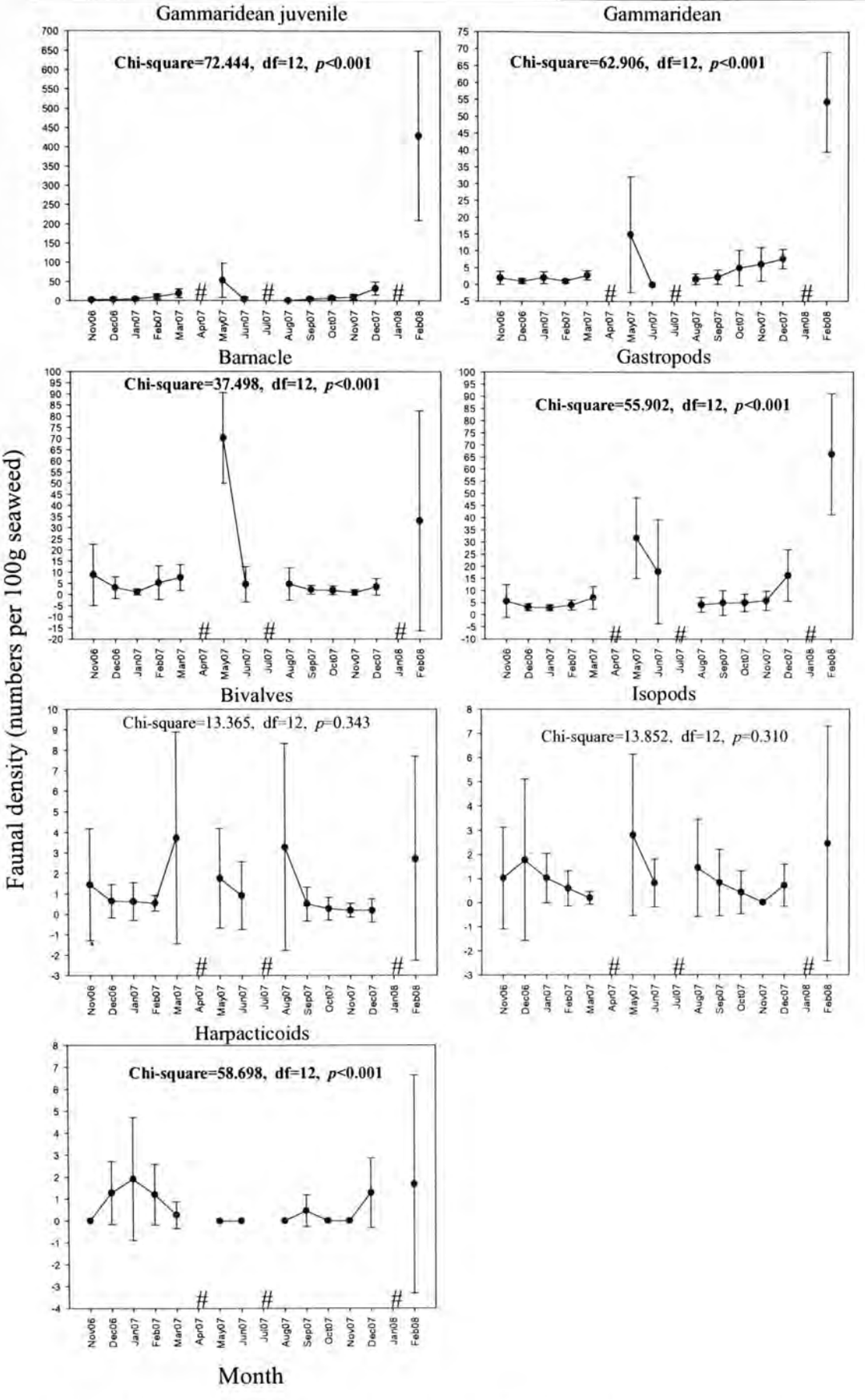


Fig. 4.16 Temporal changes in mean (± S.D.) density of common taxonomic groups in LLT. Kruskal Wallis test indicates significant temporal differences in the density of gammarideans and their juvenile, barnacle, gastropods and harpacticoids. No sampling was performed in Apr07, Jul07 and Jan08 (marked as #).

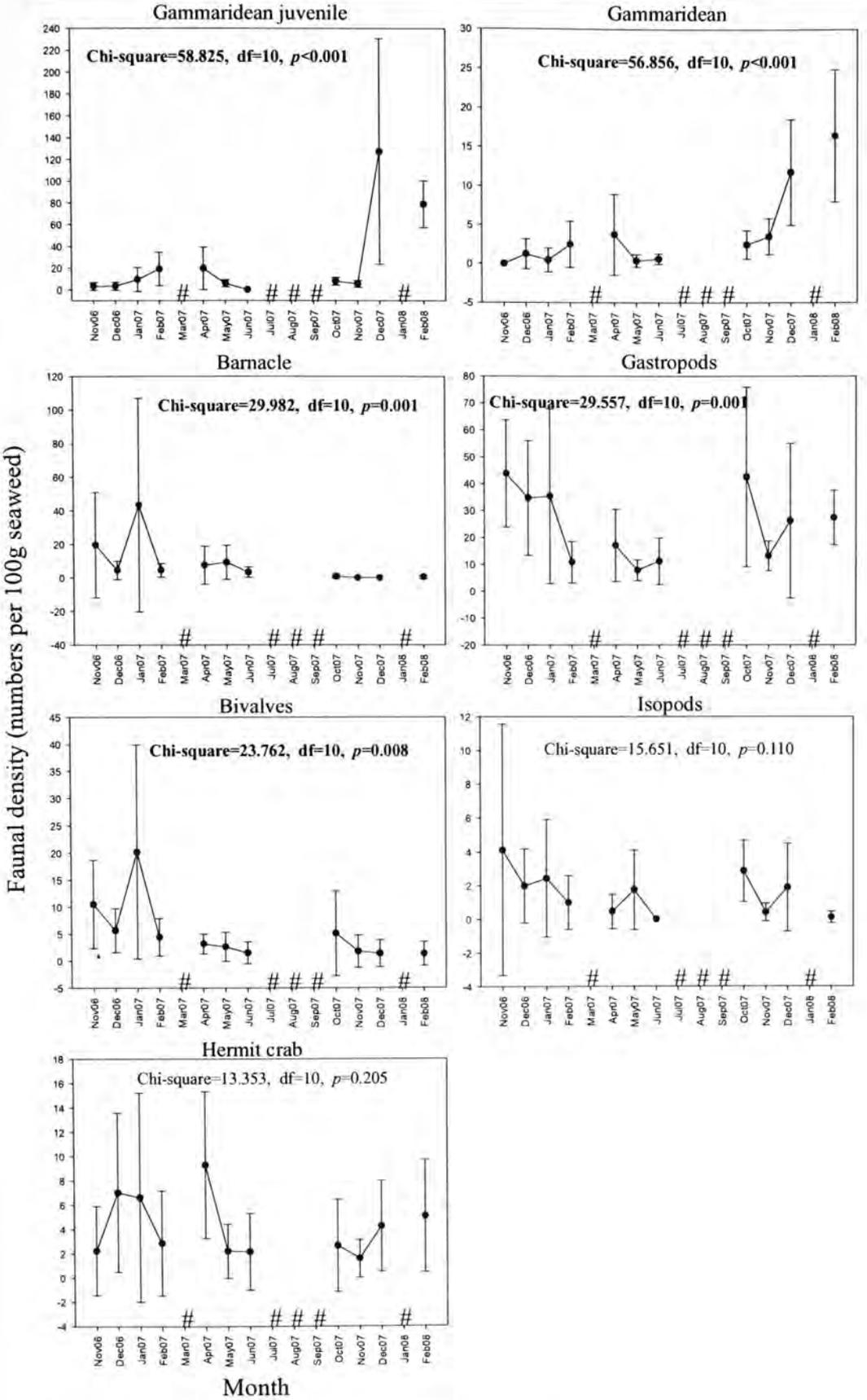


Fig. 4.17 Temporal changes in mean (± S.D.) density of common taxonomic groups in LLS. Kruskal Wallis test indicates significant temporal differences in the density of gammarideans and their juveniles, barnacle, gastropods and bivalves. No sampling was performed in Mar, Jul, Aug, Sep07 and Jan08 (marked as #).

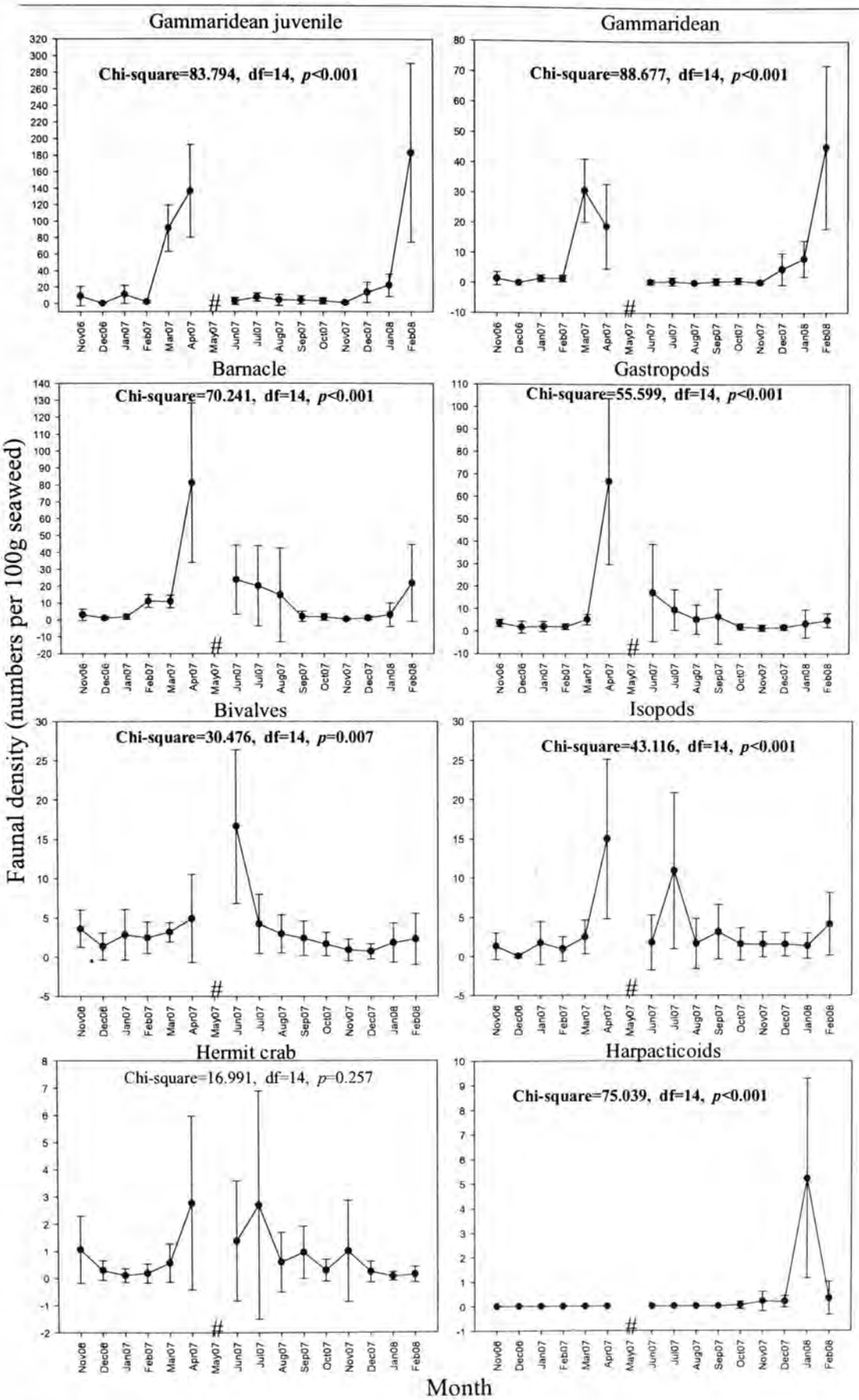


Fig. 4.18 Temporal changes in mean (± S.D.) density of common taxonomic groups in LFN. Kruskal Wallis test indicates significant temporal differences in density of all fauna groups but not hermit crab. No sampling was performed in May07 (marked as #).

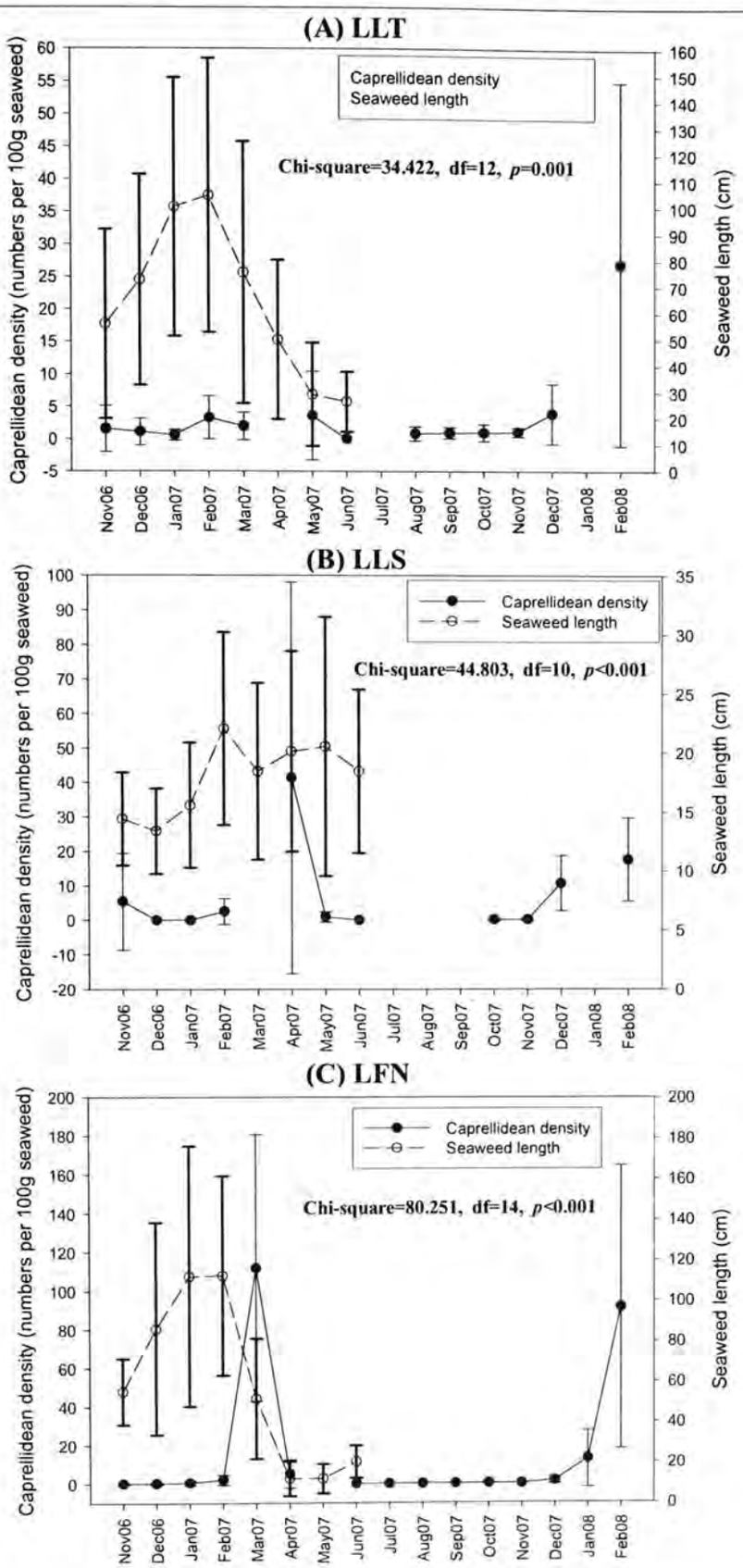


Fig. 4.19 Temporal changes in mean (± S.D.) caprellidean density and seaweed length between months in **(A)** LLT, **(B)** LLS and **(C)** LFN. Kruskal Wallis tests indicate significant differences in caprellidean density among months.

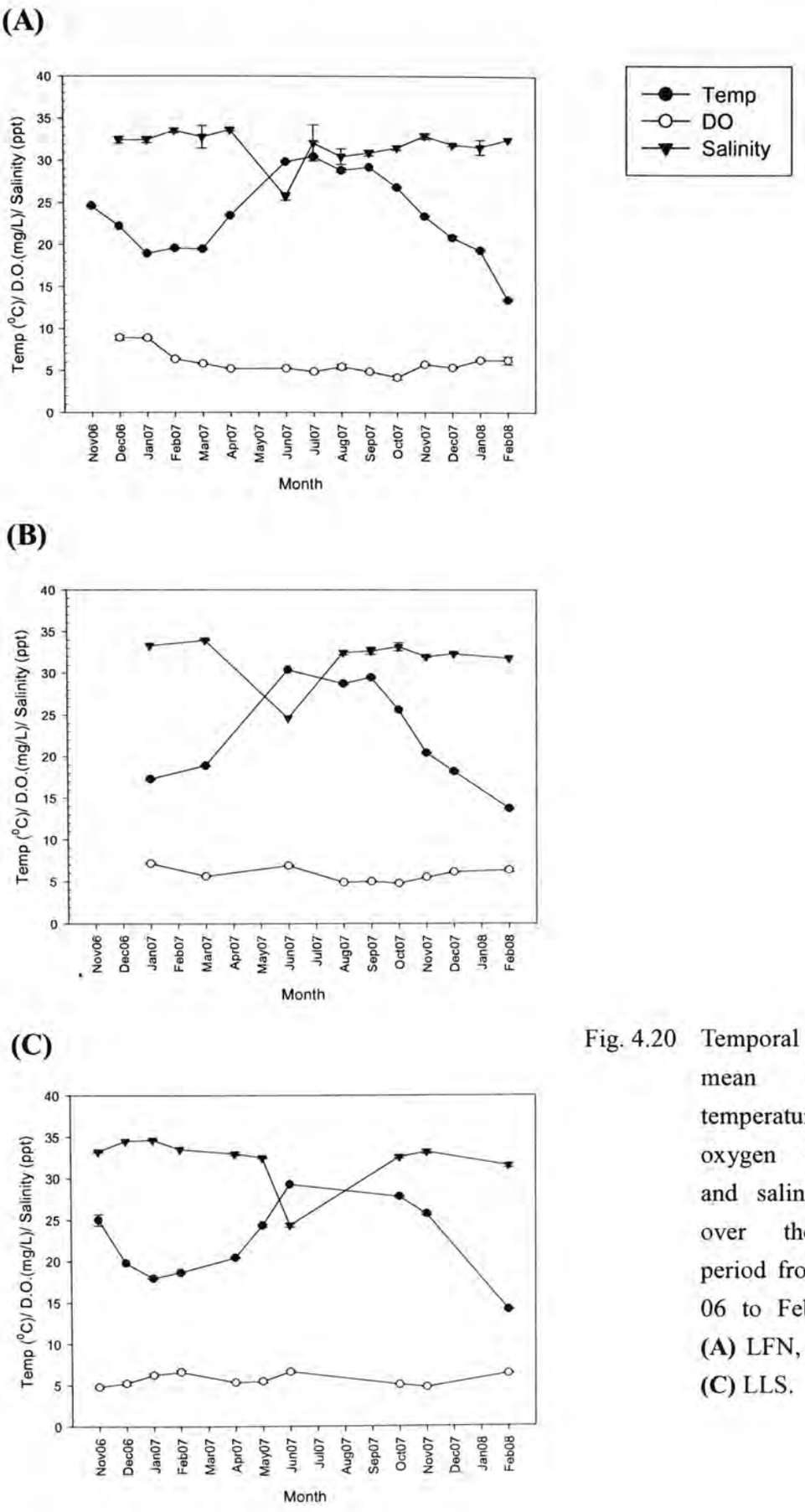


Fig. 4.20 Temporal changes in mean (± S.D.) temperature, dissolved oxygen concentration and salinity (n = 3) over the sampling period from November 06 to February 08 in **(A)** LFN, **(B)** LLT and **(C)** LLS.

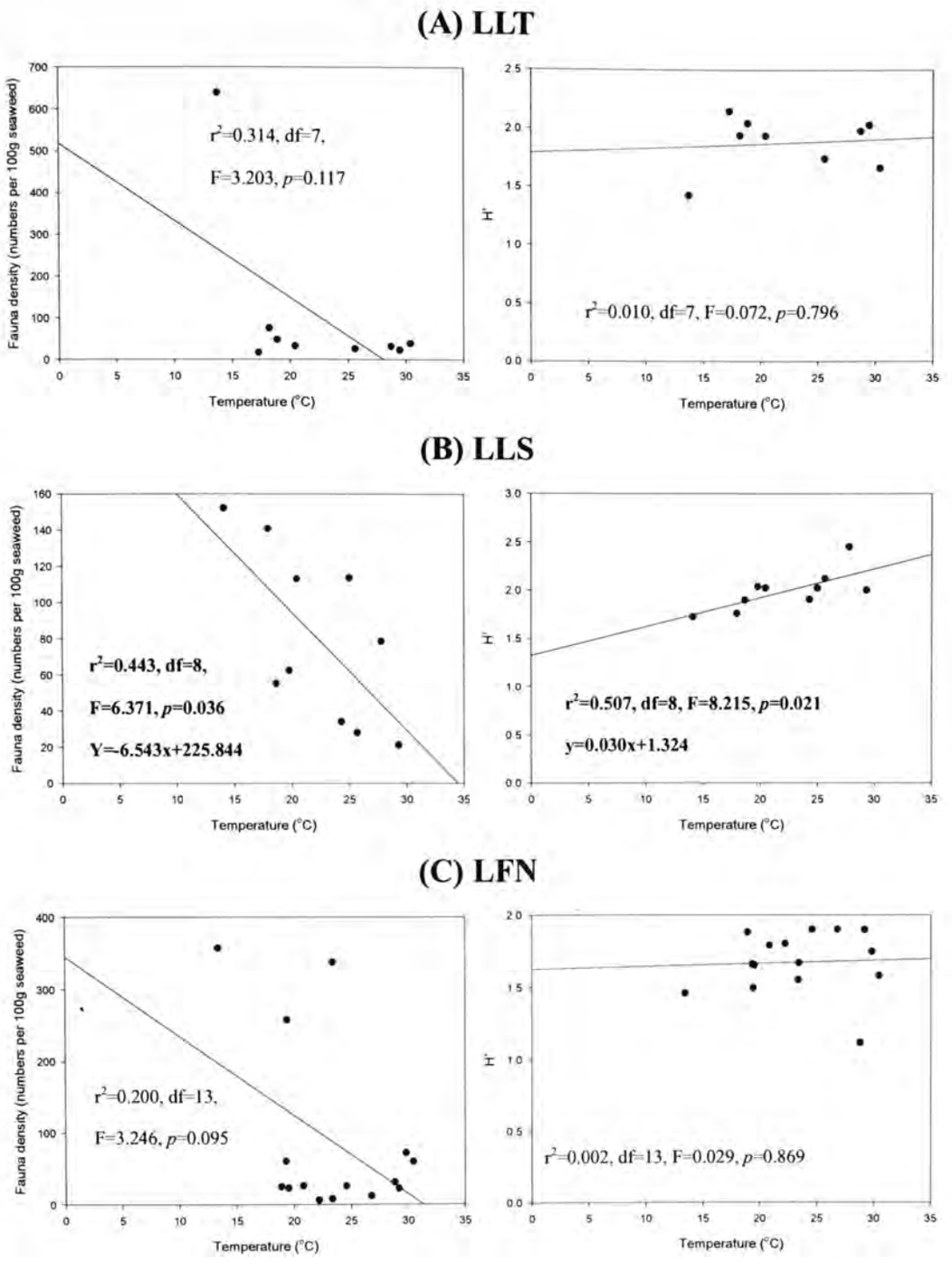


Fig. 4.21 Relationship between temperature and epiphytic faunal density and Shannon diversity index (H') in **(A)** LLT, **(B)** LLS and **(C)** LFN. Regression analyses indicate only relationships in LLS were statistically significant. Only equation for the significant relationship shown.

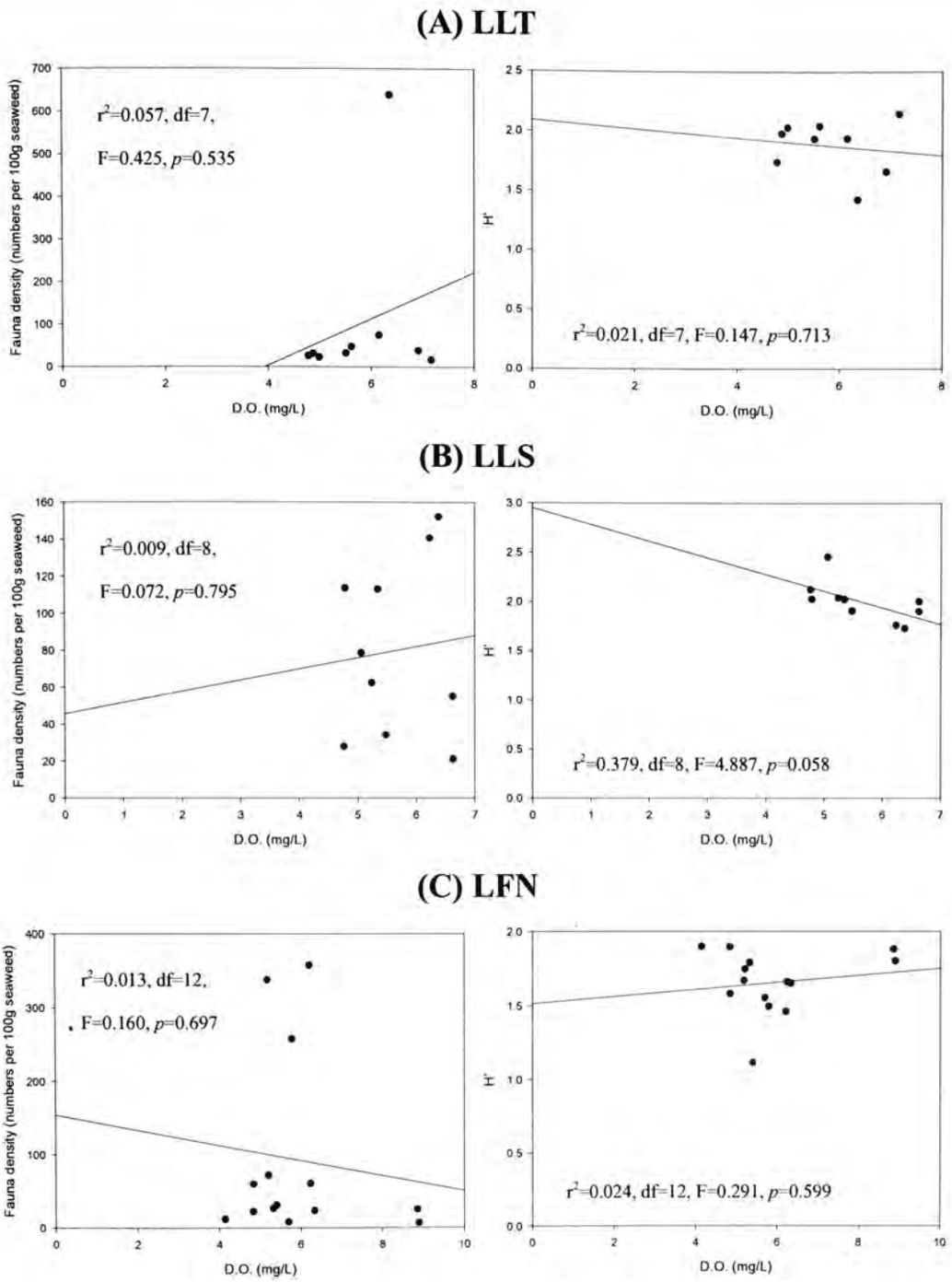


Fig. 4.22 Relationship between dissolved oxygen concentrations and epiphytic faunal density and Shannon diversity index (H') in **(A)** LLT, **(B)** LLS and **(C)** LFN. Regression analyses indicate all relationships to be statistically not significant. Regression equations not shown.

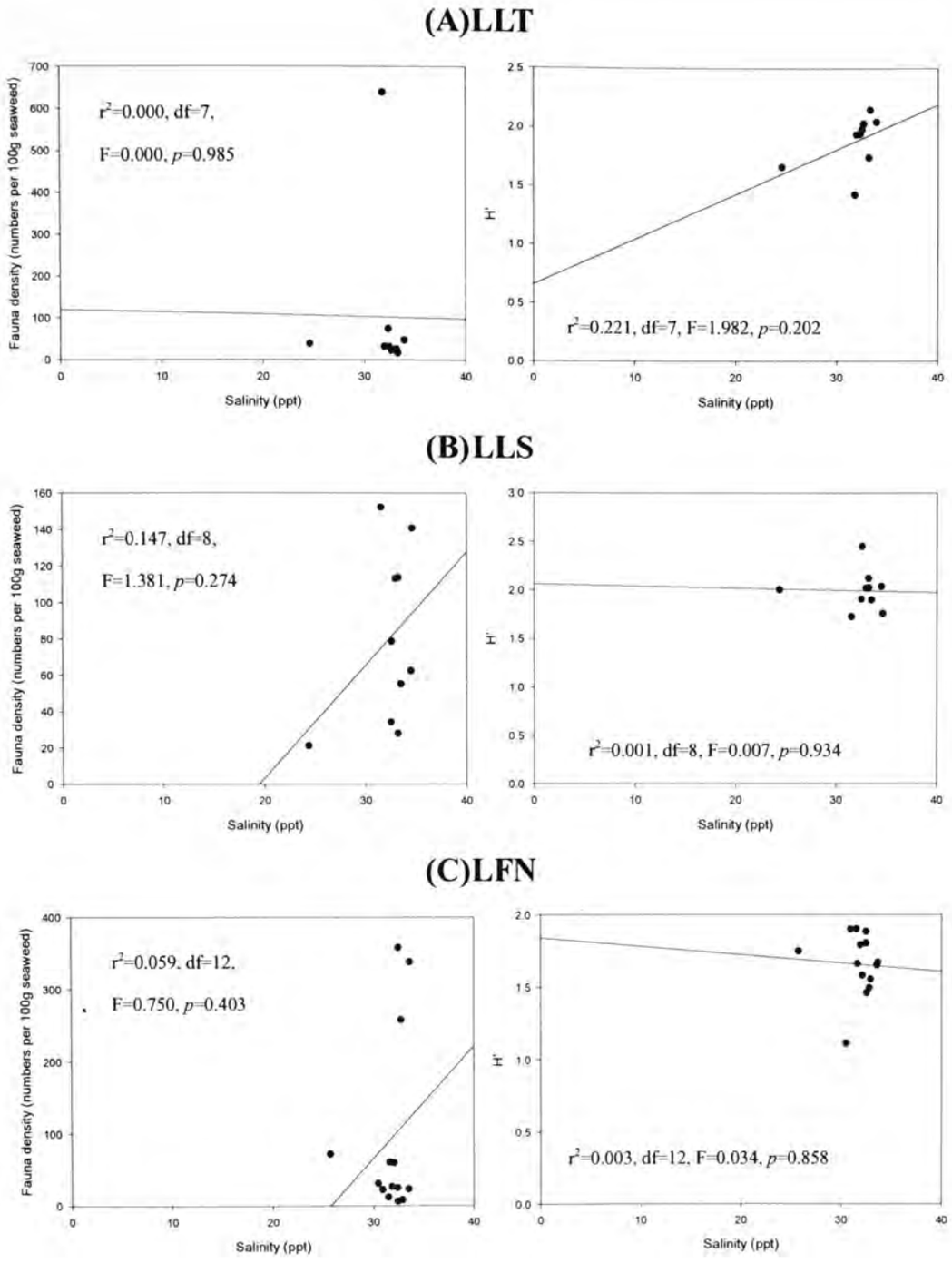


Fig. 4.23 Relationship between salinity and epiphytic faunal density and Shannon diversity index (H') in **(A)** LLT, **(B)** LLS and **(C)** LFN. Regression analyses indicate all relationships to be statistically not significant. Regression equations not shown.

Chapter 5

Relationship of Epiphytic Faunal Assemblages with the Structural Complexity of Seaweed *Sargassum siliquastrum*

5.1 Introduction

Habitat complexity, or spatial heterogeneity, is an environmental feature generally believed to affect species abundance and composition directly (Pielou 1975, Pianka 1978). Habitat complexity refers to quantitative characteristics in the form of surface area (Stoner 1983, Dean and Connell 1987a), plant height and degree of branching (Edgar 1983c, Dean and Connell 1987a) or qualitative attributes in the form of food sources, types of habitat and attachment sites as reflected by biomass (Heck and Wetstone 1977, Heck and Orth 1980, Stoner 1980, Stoner and Lewis 1985). Specifically, habitat architecture is defined by the number, size, shape, and arrangement of habitable spaces and structures for a given organism (Hacker and Steneck 1990). Enhanced habitat complexity produces increased number of distinct niches and, consequently, allows more species to coexist (Johnston and Odum 1956, MacArthur and MacArthur 1961, Kohn and Leviten 1976, Cody 1981, Bell and Coen

1982, Hicks 1982, Menge *et al.* 1985).

Macroalgal structural complexity has been one of the attributes considered in determining the structure of its associated faunal assemblage in terms of abundance and species diversity throughout a year (Hicks 1977, Stoner 1979, 1982, Edgar 1983a, 1990, Gunnill 1983, Lewis 1984, Bell and Westoby 1986, Russo 1987, Hacker and Steneck 1990, Taylor and Cole 1994, Jones and Boulding 1999, Aikins and Kikuchi 2001, Lippert *et al.* 2001, Danovaro and Fraschetti 2002, Norderhaug 2004, Hauser *et al.* 2006, Schmidt and Scheibling 2007) or along the algal successional stages (Dean and Connell 1987a, 1987b). Lippert *et al.* (2001) indicated that the major factors influencing the composition of macroalgal associated epifauna were the overall growth form and the three-dimensional thallus structure of the macroalgae. Gee and Warwick (1994a, b) showed that epiphytic faunal abundance was related to the size and structure of the algae, expressed in their fractal dimension, with more epiphytic fauna occupying algae with greater complexity. The finely structured seaweeds supported more animals than did coarsely structured seaweeds (Taylor and Cole 1994). However, plants with high complexities, expressed as seaweed surface area to biomass ratio, did not necessarily support the highest epifaunal abundances or species richness (Lewis 1984, Russo 1990). This implied that the relationships

between algal complexity and the fauna distribution and abundance were neither simple nor direct (Bell and Westoby 1986).

Habitat complexity has been shown to mediate processes in marine phytal invertebrate communities, such as predation (Heck and Wetstone 1977, Crowder and Cooper 1982, Coull and Wells 1983, Edgar 1983a, 1983b, Leber 1985, Choat and Ayling 1987, Russo 1987, Nelson and Bonsdorff 1990, Jenkins and Hamer 2001), competition (Coen *et al* 1981, Edgar 1983c, Gunnill 1984, Marx and Herrnkind 1985), food availability (Werner and Hall 1977, Marx and Herrnkind 1985), and recruitment (Moore 1977, Steger 1987, Lippert *et al.* 2001). Edgar (1983a) attributed partly the quantitative differences in the abundances of animal species on algae of different shapes to the close correspondence between algal shape and faunal size structure. Small animals, particularly amphipods, were more likely to be present on filamentous algae than on plants with wide thalli, while larger animals showed the opposite response. This relationship possibly resulted from changes in the predation pressure by fish foraging amongst algae of different shapes.

Apart from algal shape and branching degree, biomass of the macroalgae has also been shown to cast a direct positive effect on the density as well as species richness

of the associated macrofauna (Mukai 1971, Stoner 1980, Gunnill 1982, Stoner and Greening 1984, Stoner and Lewis 1985, Russo 1989, Ansari 1999, Attrill *et al.* 2000, Aikins and Kikuchi 2001, Albertoni *et al.* 2001, Danovaro and Fraschetti 2002, Leite and Turra 2003, Kraufvelin *et al.* 2006). Fauna abundance associated with the floating alga *Sargassum serratifolium* had a positive correlation with the algal standing crop (Mukai 1971). The species richness was also positively related to clump size of the floating seaweed (Ingólfsson 1995, Ólafsson *et al.* 2001).

In contrast to studies on the effects of macroalgal structural complexity and biomass on the associated faunal composition, the significance of within-plant zonation of fauna in macroalgal communities was less appreciated and hence was not investigated extensively worldwide. Vertical microhabitat stratification in terrestrial vegetation has been demonstrated to be due to resource partitioning by the associated terrestrial organisms (Edington and Edington 1972, Schoener 1974). In comparison, microhabitat selection in aquatic vegetation appeared to be based on certain aspects of the habitat quality, such as habitat heterogeneity and architecture, available food and living space (Heck and Wetstone 1977, Lewis 1984, Virnstein *et al.* 1984, Leber 1985, Edgar and Robertson 1992, Viejo and Aberg 2003, Christie *et al.* 2003). A highly complex habitat is thought to increase the number of niches available and thus

allow the coexistence of potentially competing species through the use of separate microhabitats within a complex system (Beukers and Jones 1997). Hicks (1982) stated that as algal structures became more complex, the structure was partitioned vertically and horizontally, allowing more species to coexist through finer resource utilization and tighter species packing. In addition to variation in within-plant complexity, differential internal production of defensive compounds in a marine alga can significantly affect the pattern of herbivory on the plant (McKey 1979, Steinberg 1984), and in turn can influence the distribution of species along the plant. Different plant parts are allocated with variable nutritional values and chemical content, depending on the value of each portion and that portion's relative risk of herbivore attack (Rhoades 1979, Hay 1984, Cronin and Hay 1996, Pavia and Åberg 1996). Steinberg (1984) correlated lower consumption rate of the herbivorous snail *Tegula funebralis* on the reproductive fronds (sporophylls) of the kelp *Alaria marginata* to higher concentrations of internal phenolic compounds in these fronds when compared with that in the vegetative blades. Pavia *et al.* (1999) demonstrated that the pronounced preference of adult isopod *Idotea granulosa* for the meristematic apices of the brown alga *Ascophyllum nodosum* was probably due to higher nutrient content of the younger apices over older parts rather than the lower concentrations of phlorotannins in the meristematic apices (Pedersen 1984).

In this study, the effects of the primary components of habitat structural characteristics, namely length, branch number, biomass (i.e. surface area), of the brown macroalga *Sargassum siliquastrum* on the associated faunal assemblage structure were investigated. Furthermore, the within-plant zonation of epiphytic faunal assemblage was also examined to study the effects of seaweed micro-scale structural complexity and resource allocation, e.g. possible presence of defense chemicals, on the faunal structure and distribution.

5.2 Materials and Methods

5.2.1 Sample collection

Samples used in the present study were collected in the same way as those used to examine the effect of algal structural complexity on faunal assemblage. More details of sampling methodology are given in Chapter 4 Section 4.2.1.

For the investigation on within-plant faunal zonation, epiphytic faunal samples on *Sargassum siliquastrum* were collected from two sites: Lung Lun Tsui (LLT) and Lo Fu Ngam (LFN) from September to February (i.e. during algal rapid growth,

reproductive and dieback stages) in the years 2006 and 2007. For easy reference, samples collected during the rapid growth stage (i.e. from September to November) in the year 2006 were denoted as '06 Rapid growth' and those in the year 2007 as '07 Rapid growth', and so on. As sizes of the algal individuals varied considerably in each of the different algal growth stages, an initial exploration was made into the algal bed each time to find out the largest and smallest sizes of individual plants. Individual algal plants were then categorized into three size groups, namely small (those about the size of the smallest individuals), medium (those in between small and large sized individuals) and large (those about the sizes of the longest individuals) in each growth stage. For each size class, six replicate plants were picked haphazardly with their length measured. A total of 18 replicate plants were obtained in each sampling period. Mean length of each size class during each seaweed growth stage in both sites is illustrated in Table 5.1. Zonation within individual plants was pre-determined as follows: For individuals belonging to the small size group, the whole plant was regarded as one zone (=lower zone). Plant of medium size was divided into two zones. That part of the plant about the height of the longest small sized plant was classified as lower zone; the rest of the plant above this height was classified as middle zone (see Figure 5.1). For large sized plants, the lower zone was that part of the plant about the size of the longest small plant; the middle zone was

that part of the plant above the lower zone and up to the part about the size of the longest medium sized plant; and the upper zone was the rest of the plant above the middle zone (Figure 5.1). During each sampling, a labeled bag (mesh size = 125 μm) pre-marked with corresponding zones was used to collect the individual plant together with its associated faunal assemblages. For a large sized plant, for example, the whole plant would be enclosed initially by the mesh bag pre-marked with three zones. A cord was used to tighten the border of each zone so as to seal and enclose all the faunal assemblages associated with each zone. The whole plant was then brought back to the laboratory, cut into three parts (= three zones) while still enclosed in the mesh bag and with all the associated faunal individuals from each zone collected in separate bucket (see more details below).

5.2.2 Data acquisition

To study the structural complexity of individual algal plant, the length, fresh weight and number of branches (up to tertiary level) of each plant were determined in the laboratory after removal of all its associated fauna as described in Chapter 4 Section 4.2.2. To investigate the within-plant zonation of the faunal assemblages, each zone of *Sargassum siliquastrum* was initially immersed in a bucket containing 6L

freshwater with 10ml formalin for 2 minutes to stun the epiphytic fauna, followed by vigorously washing for 2 minutes. Washing was carried out twice for each part. Detached faunas were then sieved through a mesh sieve of 500μm. The sampling bags and buckets were also rinsed with formalin freshwater and then sieved through the 500μm mesh sieve to collect any remaining fauna. The epiphytic faunas obtained were fixed in 70% alcohol immediately after sieving and stored in labeled 250mL vial bottle. All animals were identified to the possible lowest taxon level (i.e. family, genus or species level) following Huang (2001) and counted using a dissecting microscope. Plant length, number of branches (up to tertiary level), fresh weight, and surface area of fronds and branches were measured for each zone. Surface areas of fronds and branches were obtained using the program Image-Pro Plus 5.0. Seaweed length and branch number were regarded as indication of structural complexity; while seaweed fresh weight and surface area as biomass indicator.

Epiphytic faunal abundance was expressed as numbers of individuals of all species. Species richness in this study referred to number of species and taxon groups. Diversity was calculated and expressed as species richness and Shannon Diversity Index H' (see Chapter 2 for more details). Faunal density was expressed as number of individuals per 100g of algal wet weight. Averages of faunal density and species

richness, as well as seaweed fresh weight and branch number, in each zone were reported with standard deviation for the rapid growth, reproductive and dieback stages. The proportional abundance of the common epiphytic faunal groups collected from each zone was compared by calculating the percentage of individuals belonging to the same taxonomic group over total number of individuals. Association degree of the common groups was obtained by calculating the mean percentage of number of individuals in each zone in proportion to total abundance of that group in all zones.

5.2.3 Data analysis

In the study of structural complexity, relationships between epiphytic faunal assemblage, in terms of faunal abundance and species richness (plus Shannon Diversity Index H' as presented in the Appendix), and macroalgal physical parameters, namely length, branch number and fresh weight, were tested by regression analyses respectively across all seaweed growth stages. Moreover, the relationship among macroalgal physical features, namely fresh weight, length, branch number and surface area, during each of the seaweed growth stages was also evaluated using regression analyses. Both linear and non-linear regression analyses were attempted in evaluating these relationships in order to obtain the best fit of the

regression line that represented the largest proportion of the data points (i.e. highest R^2 values).

In the investigation on within-plant zonation of the epiphytic faunal community structure, the abundance and species composition of the epiphytic fauna of each zone were subjected to non-metric multidimensional scaling ordination (MDS) and cluster analysis using the Bray-Curtis similarity measure. Two-dimensional MDS plots were displayed if the stress value was below 0.2, or a 3-dimensional MDS plots were shown instead if stress value of the corresponding 2-dimensional plots was larger than 0.20. ANalysis Of SIMilarities (ANOSIM) was employed to test the statistic for significant differences ($p<0.05$) among zones and, SIMilarity of PERcentages (SIMPER), to identify the discriminating taxa between groups. Standardization and fourth-root transformation was performed on the abundance data prior to the analyses. All community analyses were carried out using PRIMER 6 (Clarke and Warwick 2001).

To evaluation significant among-zone differences in epiphytic fauna density and species richness, as well as seaweed biomass and branch number, either parametric one-way ANOVA or non-parametric Kruskal-Wallis test was performed. All

statistical analyses were performed using SPSS 13.0 for Windows (SPSS Inc., USA). All data were tested for normality by Kolmogorov-Smirnov test or homogeneity of variance by Levene Median test. Transformation of the data was carried out if the parametric assumptions were not met. Non-parametric analyses were used instead if transformations of data still failed to satisfy the assumptions of parametric tests. The significance level (p value) of all statistical analyses was set at 0.05.

5.3 Results

5.3.1 Effects of Macroalgal Structural Complexity on the Associated Epiphytic Faunal Assemblage Structure

5.3.1.1 Effects on Epiphytic Faunal Abundance

Figures 5.2-5.4 display the relationship between mean seaweed length and mean abundance of the associated epiphytic faunal assemblage in the three study sites. In general, no consistent patterns of relationship were observed throughout the sampling period, except that epiphytic faunal abundance was significantly weakly related with seaweed length during 07 rapid growth, 07 reproductive and 08 dieback stages of *S. siliquastrum* at LLT (Figure 5.2); and 06 rapid growth and 07 slow growth stages of

S. siliquastrum at LFN (Figure 5.4).

Mean epiphytic faunal abundance generally increased with increase in mean seaweed fresh weight during different *Sargassum siliquastrum* growth stages. Significant positive relationship between faunal abundance and seaweed fresh weight was detected in all growth stages other than that during 06 rapid growth and 07 dieback stages at LLT (Figure 5.5); 06 rapid growth, 07 rapid growth and 08 dieback stages at LLS (Figure 5.6); and 06 rapid growth and 07 slow growth stages at LFN (Figure 5.7).

For the relationship between mean seaweed branch number and mean abundance of the associated epiphytic faunal assemblage, no general consistent trends were observed throughout the sampling periods (Figures 5.8-5.10). However, faunal abundance was significantly positively related with seaweed branch number during 06 reproductive, 07 rapid growth, 07 reproductive and 08 dieback stages at LLT (Figure 5.8); 07 rapid growth stage at LLS (Figure 5.9) and 07 slow growth stage at LFN (Figure 5.10).

5.3.1.2 Effects on Epiphytic Faunal Species Richness

No consistent patterns of relationship were detected between mean seaweed length and mean species richness of the associated epiphytic faunal assemblage in the three study sites throughout the sampling periods (Figures 5.11-5.13). A few exceptions being the statistically significant but weak, (i.e. low r^2 values) positive relationship observed in 07 slow growth stage at LLT (Figure 5.11), 06 rapid growth stage at LLS (Figure 5.12) and 07 slow growth stage at LFN (Figure 5.13).

Figures 5.14-5.16 demonstrates the relationship between mean seaweed fresh weight and mean species richness of the associated epiphytic faunal assemblage in the three study sites. This relationship was generally positive. Species richness increased with increase in seaweed fresh weight over majority of the *Sargassum siliquastrum* growth stages. This positive relationship was particularly better defined during reproductive and dieback stages, as indicated by the relatively higher values of the coefficient of determination (r^2) recorded for the regression line best fitted for data from these periods.

In most seaweed growth stages, mean species richness of the associated epiphytic

faunal assemblage in the study sites also increased with increase in mean seaweed branch number (Figures 5.17-5.19). Significant positive relationship was spotted with *S. siliquastrum* during its 06 reproductive, 07 slow growth, 07 rapid growth and 08 dieback stages at LLT (Figure 5.17); and 07 slow growth and 07 reproductive stages at LFN (Figure 5.19).

The relationship between seaweed structural complexity and mean Shannon Diversity Index H' as well as Evenness Index J was not obvious. In most cases, the relationship was not statistically significant (see Appendix Figures A5.1-A5.9).

5.3.1.3 Relationship among Parameters of *Sargassum siliquastrum*

Mean seaweed fresh weight and mean length (Figure 5.20 A), together with mean seaweed thalli surface area and mean fresh weight (Figure 5.20 B), were significantly positively related among each other. The fresh weight increased with an increase in algal length and thalli surface area with fresh weight. Seaweed branch number related more closely with fresh weight than with length, as implied by the comparatively greater coefficient of determination (r^2 value) obtained for the former (Figures 5.20 B and C). In both cases, seaweed branch number generally increased

with increase in seaweed fresh weight and length.

5.3.2 Within-plant Zonation of Epiphytic Faunal Assemblage Structure

In addition to the MDS ordination and ANOSIM analyses (Figures 5.21 and 5.22), SIMPER analyses were performed to determine the discriminating taxa among groups if significant among-zone differences in faunal assemblage were detected. In LLT (Figure 5.21), significant difference in epiphytic faunal assemblages among zones was detected in 07 dieback stage in which harpacticoids, barnacles and isopods were the primary discriminating taxa between lower and middle zones; hermit crab, isopods and barnacles between lower and upper zones; harpacticoids, gastropod larvae and gammaridean juveniles between middle and upper zones. Significant difference with slight similarity in faunal community structure among zones was obtained during 08 dieback stage in which barnacles were the leading differentiating taxon between lower and middle zones as well as between lower and upper zones; gammaridean amphipods and gastropod larvae between middle and upper zones. In LFN (Figure 5.22), significant disparity with slight similarity in epiphytic faunal assemblage among zones was revealed in 06 reproductive stage in which barnacles were the major discriminating taxon between lower and middle zones as well as

between lower and upper zones; caprellideans and gastropod larvae between middle and upper zones. Significant difference in faunal community structure among zones was detected in 07 dieback stage in which gastropod larvae, barnacles and gammaridean of *Guernea* spp. were the principal differentiating taxa between lower and middle zones as well as between lower and upper zones; and gastropod larvae between middle and upper zones. Epiphytic faunal assemblages among zones exhibited considerable disparity with slight similarity in 08 dieback stage in which barnacles, isopods and gammaridean of *Guernea* spp. were the primary discriminating taxa between lower and middle zones as well as between middle and upper zones; *Lophogaster pacificus*, harpacticoids and fish juvenile *Petroscrites breviceps* between middle and upper zones.

5.3.2.1 Within-plant Distribution of Epiphytic Faunal Density

Figure 5.23 illustrates the mean epiphytic faunal density in each zone of *Sargassum siliquastrum* in each growth stage at LLT. In 06 and 07 rapid growth stages, mean (± S.D.) epiphytic faunal density in the lower zone was the highest at 43.75 ± 28.76 and 46.45 ± 33.03 individuals per 100g seaweed respectively, followed by that in the middle zone. Lowest density was recorded in the upper zone. In 06 and 07

reproductive stages, faunal density in the upper zone, at 45.10 ± 63.76 and 109.54 ± 50.71 individuals per 100g seaweed respectively, was the greatest amongst the three zones while that in the lower zone was the lowest. In 07 and 08 dieback stages, middle zone of the seaweed attained the highest faunal density at 22.19 ± 21.04 and 704.63 ± 221.69 individuals per 100g seaweed respectively, followed by that in the upper and lower zones. However, no statistically significant among-zone differences in epiphytic faunal density were found in all these growth stages.

Figure 5.24 shows the mean epiphytic faunal density in each zone of *Sargassum siliquastrum* in each growth stage at LFN. In 06 and 07 reproductive stages, mean (± S.D.) faunal density was at its maximum at 32.59 ± 17.60 and 79.36 ± 33.42 individuals per 100g seaweed respectively in the lower zone, followed by that in the upper and middle zones. In 07 dieback stage, faunal density in the upper zone was the highest at 116.60 ± 16.81 and the lowest in the lower zone at 69.54 ± 17.02 individuals per 100g seaweed. In 08 dieback stage, middle zone obtained the greatest faunal density at 412.35 ± 438.08, followed by lower zone at 316.45 ± 110.67 and then upper zone at 246.61 ± 151.70 individuals per 100g seaweed. In 07 rapid growth stage, faunal density in the lower zone at 37.59 ± 54.22 individuals per 100g seaweed was significantly the highest amongst the three zones. Statistically significant

among-zone difference in epiphytic faunal density was only found in 07 rapid growth stage but not in the other growth stages.

5.3.2.2 Within-plant Distribution of Epiphytic Species Richness

In the 06 and 07 rapid growth stages of *Sargassum siliquastrum* at LLT, mean (± S.D.) species richness in the lower zone of the algae was the highest at 10.17 ± 3.66 and 8.44 ± 4.77 respectively (Figure 5.25). Significant among-zone difference in species richness was obtained in 06 rapid growth stage but not in 07 rapid growth stage. In 06 and 07 reproductive stages, lower zone of the algae supported the highest species richness at 13.08 ± 3.53 and 16.00 ± 2.76 respectively, followed by the middle zone with the lowest species richness found in the upper zone. Significant disparity in species richness among zones was detected in 06 reproductive stage in which species richness in the lower zone was distinctly different from the statistically similar species richness in both middle and upper zones. In 07 and 08 dieback stages, species richness in the lower zone, at 14.00 ± 3.69 and 19.33 ± 3.33 respectively, was significantly the highest among the three zones. Significant among-zone difference in species richness was detected in both these stages in which species richness in the middle and upper zones were statistically similar while that in the lower zone was

statistically significantly different from those in the other two zones.

Figure 5.26 shows the mean epiphytic faunal species richness in each zone of *Sargassum siliquastrum* at LFN. In 06 and 07 reproductive stages, mean (± S.D.) species richness in the lower zone at 12.22 ± 4.30 and 15.58 ± 4.46 respectively was significantly the highest among the three zones. In 07 and 08 dieback stages, lower zone attained the greatest species richness at 14.00 ± 3.69 and 19.33 ± 3.33 respectively, with species richness in the lower zone being significantly different from the statistically similar middle and upper zones. In 07 rapid growth stage, species richness in the lower zone at 7.89 ± 5.09 was significantly the highest, followed by that in the upper and middle zones.

5.3.2.3 Within-plant Distribution of Epiphytic Faunal Species Composition

In LLT, species composition in the lower zone of *Sargassum siliquastrum* plants was more diverse when compared with that in the middle and upper zones throughout the seaweed growth stages (Figure 5.27). This corroborated the patterns shown in Figure 5.25 in which species richness in the lower zone was found to be the highest. In the seaweed lower zone (Figure 5.27 A), the numerically important faunal groups were

consistently the gammaridean juveniles (accounting for up to 30-70% of the total population), gastropods (10-30%), barnacles (5-30%) and isopods (2-11%); whereas brittle stars (5-7%) were important only in the rapid growth stages. In the middle zone (Figure 5.27 B), the dominant groups were consistently gastropods (contributing up to 3-60% of the total population), gammaridean juveniles (20-40%), harpacticoids (3-30%); while isopods (14%) were important only in 06 rapid growth stage, caprellidean (6-20%) in the reproductive stages, and bivalves (13%) in 07 dieback stage. In the upper zone (Figure 5.27 C), the abundant groups were constantly the gammaridean juveniles (making up to 40-70% of the total population) and gammaridean amphipod (10-30%); while harpacticoid (20-24%) were important only in the reproductive and dieback stages, caprellidean (7-12%) in the reproductive stages and lophogaster (5-10%) in 06 reproductive and 07 rapid growth stages.

Figure 5.28 presents the association degree of common epiphytic faunal groups among seaweed zones in each growth stage at LLT. Hyperiidean amphipods, brittle stars, sea urchins and peanut worms were entirely associated with the lower zone of the seaweeds. Brachyurans and macrurans resided 100% in the lower zone during the 06 reproductive and 07 dieback stages. Tubeworms and bivalves were wholly associated with the lower zone but distributed uniformly between lower and middle

zones in 07 reproductive and 07 dieback stages. Hermit crabs were frequently allied with the lower zone in most of the time but were encountered in both lower and middle zones in reproductive stages. Gammaridean amphipods and their juveniles, caprellideans, gastrpods and isopods were encountered in all three zones but were more closely associated with the lower zone during most of the growth stages. Gammarideans and their juveniles were more evenly distributed among the three zones in 07 reproductive stage. Polychaetes and barnacles mostly resided in the lower zone but were found among the three zones during rapid growth and reproductive stages. On the other hand, fish juveniles were entirely associated with the middle zone in 06 reproductive stage. Lophogasters resided completely in the middle zone in 06 rapid growth, 07 reproductive and 08 dieback stages but were evenly distributed among the three zones in 06 reproductive and 07 rapid growth stages. Harpacticoids regularly resided in the middle or upper zone but were wholly associated with the lower zone in 08 dieback stage. Calanoid copepods were completely associated with the upper zone in 07 reproductive stage.

In LFN, species composition of the epiphytic fauna in the lower zone of *S. siliquastrum* was also relatively more complex when compared with that in the middle and upper zones throughout the seaweed growth stages (Figure 5.29). This

was in accordance with the patterns observed in Figure 5.26 in which species richness in the lower zone was the highest among the three zones. In the lower zone (Figure 5.29 A), the consistent dominant groups were the gammaridean juveniles (accounting up to 23-54% of the total population), caprellideans (13-32%), gammaridean amphipods (5-15%), barnacles (2-21%), gastropods (2-19%) and isopods (2-15%). In the middle zone (Figure 5.29 B), the abundant groups were consistently the gammaridean juveniles (28-56%), gammaridean amphipods (6-19%), caprellideans (23-37%) and gastropods (2-26%); while isopods (29%) were important only in the 07 rapid growth stage and harpacticoids (9%) in 07 reproductive stage. In the upper zone (Figure 5.29 C), the principal dominant groups were the gammaridean juveniles (4-74%), caprellideans (3-53%) and gastropods (5-55%); whereas polychaetes (5%) were important only in the 06 reproductive stage, isopods (23%) in the 07 rapid growth stage and harpacticoids (7%) in the 07 reproductive stage.

Figure 5.30 shows the association degree of common epiphytic faunal groups among seaweed zones in each growth stage at LFN. Tubeworms and peanut worms were completely associated with the lower zone. Brachyurans and macrurans resided entirely in the lower zone in 07 rapid growth, 07 reproductive and 08 dieback stages.

Gammaridean amphipods and their juveniles, caprellideans, polychaetes, barnacles, brittle stars, gastropods, bivalves, mysids and isopods were more frequently allied with the lower zone. Hermit crabs were mostly associated with the lower zone but distributed uniformly between lower and middle zones during 07 rapid growth and 07 reproductive stages. Lophogasters mostly resided in the lower zone but were also found in the other two zones. In contrast to the fauna regularly associated with the lower zone, sea anemones were entirely associated with the middle zone. Harpacticoids were regularly distributed among middle and upper zones. Fish juveniles resided 100% in the upper zone during 07 rapid growth and 08 dieback stages while wholly associated with the lower zone in the 07 reproductive stage.

5.3.2.4 Physical Parameters Associated with Each Zone of *Sargassum siliquastrum*

Variations in the mean fresh weight of each zone of *Sargassum siliquastrum* in each growth stage at LLT and LFN are shown in Figures 5.31 and 5.32 respectively. At LLT (Figure 5.31), in 06 rapid growth stage, mean (± S.D.) seaweed fresh weight of the lower zone was the highest at 90.57 ± 63.69 g, followed by that of the upper and then the middle zones; while in 07 rapid growth stage, fresh weight of the upper zone at 117.04 ± 152.87 g was the greatest, succeeded by that of the middle and lower

zones. In 06 reproductive stage, fresh weight of the lower zone was significantly the most enormous at 301.41 ± 205.91 g, followed by that of the middle and upper zones; whereas in 07 reproductive stage, middle zone held the greatest fresh weight at 192.29 ± 165.26 g and lower zone the lowest at 105.15 ± 80.24 g. During 07 and 08 dieback stages, the fresh weight of the lower zone was consistently the greatest at 332.79 ± 239.02 g and 60.26 ± 39.36 g respectively, succeeded by that of the middle and upper zones. Statistically significant difference in fresh weight among zones was detected only in 06 reproductive stage but not in the rest of the growth stages. At LFN (Figure 5.32), in 06 and 07 reproductive stages, mean (± S.D.) fresh weight of the middle zone was the highest at 208.80 ± 206.11 g and 175.91 ± 89.78 g respectively, followed by that of the lower and upper zones, Significant among-zone difference in fresh weight was obtained in 06 reproductive stage but not in 07 reproductive stage. In 07 and 08 dieback stages, lower zone obtained the greatest fresh weight at 218.96 ± 80.67 g and 97.89 ± 42.36 g respectively while the upper zone the lowest, with significant difference in fresh weight among zones found in 07 but not in 08 dieback stages. In 07 rapid growth stage, fresh weight of the upper zone was the most enormous at 170.00 ± 133.43 g, succeeded by that of the middle and lower zones.

Figures 5.33-5.34 show the mean branch number of each zone of *Sargassum siliquastrum* in each growth stage in LLT and LFN. At LLT (Figure 5.33), in 06 rapid growth stage, the mean (± S.D.) branch number of the lower zone at 16.00 ± 7.10 was the highest, followed by that of the upper and middle zones; while in 07 rapid growth stage, branch number of the upper zone at 11.33 ± 8.89 was the highest among the three zones. In 06 reproductive stage, lower zone obtained the greatest branch number at 17.00 ± 6.93, succeeded by that of the middle and then upper zones; whereas in 07 reproductive stage, middle zone had the highest branch number at 11.75 ± 8.30 and the upper zone the lowest. In 07 dieback stage, branch number at 18.00 ± 5.29 was the greatest in the lower zone, followed by that in the middle and the upper zones; while in 08 dieback stage, branch number at 11.75 ± 1.71 in the middle zone was the highest, followed by that in the upper and lower zones. No significant differences in branch number among zones were found across all the seaweed growth stages. At LFN (Figure 5.34), in 06 reproductive stage, the lower zone attained the most number of branches at 18.89 ± 13.04, succeeded by the middle and upper zones; whereas in 07 reproductive stage, middle zone had the greatest branch number at 9.00 ± 5.58, followed by the lower and upper zones. In 07 dieback stage, branch number of the lower zone at 10.67 ± 2.88 was the highest among the three zones; while in 08 dieback stage, branch number of the upper zone

at 10.50 ± 0.71 was the highest, succeeded by that of the lower and middle zones. In 07 rapid growth stage, the upper zone held the greatest branch number at 16.50 ± 6.16, followed by the middle zone with the lower zone having the lowest. No statistically significant among-zone differences in branch number were found in all the algal growth stages.

5.4 Discussion

5.4.1 Effects of Macroalgal Structural Complexity and Biomass on the Associated Epiphytic Faunal Assemblage Structure

Brown algae of erect structure and branching form have the highest population density of amphipods and other herbivores among all the macroalgal morphologies (Hagermann 1966, Hacker and Steneck 1990, Lippert *et al.* 2001, Norderhaug 2004). In the current study, macroalgal length generally casted a relatively insignificant impact on the epiphytic faunal abundance and species richness across the growth stages of *Sargassum siliquastrum*. On the contrary, faunal abundance and species richness experienced significant positive relation with seaweed branch number, particularly during rapid growth and reproductive stages. This may be due to the

increase in the amount of habitable space available between the branches and fronds of the algae (Hacker and Steneck 1990), the provision of favourable structures for attachment (Hagermann 1966, Lippert *et al.* 2001, Norderhaug 2004) and as refuge from predators (Heck and Wetstone 1977, 1981, Heck and Thoman 1981, Nelson 1981, Crowder and Cooper 1982, Coull and Wells 1983, Edgar 1983c, Leber 1985, Russo 1987, Pfister and Hay 1988, Holmlund *et al.* 1990, Hacker and Madin 1991, Schneider and Mann 1991a, 1991b, Martin-Smith 1993, Gagnon *et al.* 2003). Reduced foraging efficiency of predators within densely vegetated areas, compared to more open areas, allowed large populations of macro-invertebrates to exist (Stoner 1972, 1982, Poore and Hill 2005). In addition to faunal abundance, species richness also increased with branch number in this study. An increase in branch number may increase the complexity of the algal structure, which could then provide particularly high between microhabitat and food source diversities (Lewis 1984, Edgar 1990). The weak correlation between branch number and faunal assemblage during dieback stage, as observed in the present study, might be due to smoothing out of structural irregularities as the plants lost their laterals, and the infilling of habitable space by loads of phytodetritus that reduced the potential niche resources (Hicks 1977).

In this study, seaweed fresh weight posed comparatively significant influence on

epiphytic faunal abundance in which faunal abundance increased with increase in seaweed fresh weight. The effect was found to be more prominent during times of rapid growth, reproduction and dieback. In a related study, seagrass biomass was found to provide an analogue for available surface area, due to the two-dimensional laminar structure of the seagrass blades. Therefore, increasing seagrass biomass provided a larger surface area for habitation by invertebrates (Russo 1990, Attrill *et al.* 2000). The same principle is applicable to the relationship between biomass and surface area of *Sargassum siliquastrum* as seaweed surface area and fresh weight displayed statistically significant positive relationship. *Sargassum siliquastrum* of higher biomass supports more epiphytes, such as periphyton, and traps detritus due to the availability of more surface area (D'Antonio 1985, Lee *et al.* 2001, Albertoni *et al.* 2001, Lippert *et al.* 2001). It thus enhances the supply of direct food source (Brenner *at al.* 1976, Heck and Wetstone 1977, Russo 1988, Edgar 1991a, 1991b, Albertoni *et al.* 2001, Leite and Turra 2003) as well as attachment space (Fretter and Manly 1977, Heck and Wetstone 1977, Hicks 1977, Heck and Orth 1980, Stoner 1980, Stoner and Lewis 1985) for herbivores and detritivores, such as harpacticoid. Apart from the increased host plant tissue and epiphytic plant, detritus abundance was significantly positively correlated with the biomass of seagrass *Zostera japonica* (Lee *et al.* 2001). The derivation of detritus from decaying plant tissues might

increase benthic production by fueling the detritivore-dominated food web through the input of phytodetritus (Edgar *et al.* 1994). Moreover, increased algal biomass can decrease wave shock and water flow, thereby reduces the rate of dislodgement of species with limited mobility or poor ability to cling to the algae, such as gastropods, bivalves, and polychaetes (Wieser 1952, Dean and Connell 1987b, Ingólfsson 1995). Mukai (1971) found that the smaller, truly phytal animal species associated with winter growing *Sargassum* had peaks of abundance in winter, while the population abundances of the larger species (echinoderms, actinians, mysids and decapods) were not synchronized with that of the standing crop. This implies that majority of the epiphytic fauna associated with *Sargassum siliquastrum* in the present study were truly phytal animal species.

Apart from faunal abundance, species richness of the epiphytic fauna was significantly positively correlated with the seagrass biomass, i.e. surface area, and detritus standing crop (Stoner 1983, Lewis 1984, Stoner and Lewis 1985, Lee *et al.* 2001). Hicks (1980) and Ólafsson *et al.* (2001) reported a significant linear correlation between size of the floating *Sargassum* clumps and species diversity of harpacticoid copepods. Russo (1990) and Attrill *et al.* (2000) proposed that the increase in species diversity with increasing seagrass biomass was a species-area

relationship. The positive relationship between macroalgal biomass and species richness was in accordance with the present data, revealing that species richness significantly increased with seaweed fresh weight, being more marked at times of seaweed reproduction and dieback. Higher species richness with increased macroalgal biomass might simply result from a stochastic function of increasing species richness with increasing number of individuals in a habitat with enhanced complexity (Stoner and Greening 1984, Dean and Connell 1987b, Ingólfsson 1995).

5.4.2 Within-plant Zonation of Epiphytic Faunal Assemblage Structure

Stoner (1980) recognized certain faunal species might actively select for particular substratum characteristics such as texture, color, shapes and availability of crevices or folds in the associated habitat. For example, many peracarid species, mostly boring amphipod *Perampithoe femorata* and isopods, showed a strongly aggregated distribution pattern, being particularly highly abundant in kelp holdfasts (Thiel and Vásquez 2000). This agreed with the present findings that species richness was consistently the highest in lower zone, including the holdfast, during rapid growth, reproductive and dieback stages of *Sargassum siliquastrum*. Hauser *et al.* (2006) explicated that the high abundance and species diversity of fauna colonizing the kelp

holdfast was attributed to increased surface area for interception and colonization (Conner and McCoy 1979, Parrish 1989, Attrill *et al.* 2000) offered by the highly complex holdfast. The structurally complex holdfast in the lower zone was found to offer better protection from physical stress (Gibbons 1988) and have high sediment trapping potential (Coull and Wells 1983, Diehl 1992), providing greater food availability for invertebrates living on the algae. Besides, the complex holdfast reduced predation by minimizing the encounter rate and contact time between predator and prey and by degrading predator foraging efficiency and capture success (Diehl 1992, Beukers and Jones 1997). In the present investigation, epiphytic faunal density generally attained the highest value in the lower zone during the rapid growth stage, in the upper zone during the reproductive stage, and in the middle zone during the dieback stage. The abundance peak at different zones was related to the occurrence of tremendous amount of dominant groups, gammaridean amphipods, caprellidean amphipods and gastropods, associated with each zone in each growth stage.

Several studies have shown that population growth of benthic species in macroalgal communities is food limited because the vast majority of these macrobenthic species are generalist feeders which can utilize a variety of detrital, plant and animal

materials (Zimmerman *et al.* 1979, Whitlach 1980, Kitting 1984, Shillaker and Moore 1987, Edgar 1990). However, some studies reported that phytal amphipods are generally not food limited (Fenwick 1976, Heck and Wetstone 1977, Van Dolah 1978, Nicotri 1980, Dean and Connell 1987a). In the current study, brittle stars, peanut worms, brachyuran and macrurans resided entirely in the lower zone of the seaweed throughout the seaweed growth stages. Gammaridean amphipods and their juveniles, caprellidean amphipods, gastropods, isopods, hermit crabs, polychaetes, tubeworms, barnacles and bivalves were ubiquitously associated with the lower zone. The close association of gammarideans, gastropods and isopods might be explicated by the affluent food source, in terms of host plant tissue, epiphytes and phytodetritus, supported by the comparatively higher seaweed biomass of the lower zones, particularly during the reproductive and dieback stages of *Sargassum siliquastrum*. Since some amphipods, such as those under the genera *Gammarus* and *Ampithoe* (Hawkins and Hartnoll 1983, Duffy 1990, Pavia *et al.* 1999), isopods (Nicotri 1980, Salemaa 1987, Pavia *et al.* 1999), and gastropods, such as *Littorina* spp. (Hawkins and Hartnoll 1983, Pavia *et al.* 1999), are herbivores feeding mostly on their associated macroalgae, increased macroalgal biomass in the lower zone provided the herbivores with enriched plant tissue, thereby enhancing the faunal fitness. In addition to the herbivores food provision, seaweed lower zone is believed to be able

to accumulate detritus from dead animals and plant tissues since holdfasts have high sediment trapping potential (Coull and Wells 1983, Diehl 1992). The lower zone also acquired greatest complexity with the highest branch number, as shown in the current study. The comparatively plenteous organic matters, coincided with the high load of phytodetritus from the host plant tissue during dieback stage, served as abundant food supply for the detritivorous caprellideans, hermit crabs, brittle stars and peanut worms. The latter two were observed to stay in holes on the macroalgal holdfasts (Brusca and Brusca 2003, Yang *et al.* 2006). Furthermore, the increased surface area as a result of the presence of high seaweed biomass in the lower zone, as shown by the previous and the present studies, functions as desirable substratum for epiphytic plant growth. The presence of macroalgal epiphytes has been shown to be one of the factors influencing the distribution of mobile epifauna, such as gammaridean amphipods (Johnson and Scheibling 1987, Schneider and Mann 1991b, Pavia *et al.* 1999), since epiphytes served as food source (Pavia *et al.* 1999) and provided a more suitable substratum for grasping than the flat-shaped fronds (Taylor and Cole 1994). Positive interactions between co-existing herbivores might be present. Viejo and Arrontes (1992) demonstrated that superficial wounds inflicted by isopods could facilitate the feeding of gammarideans on the seaweed *Fucus vesiculosus*.

In addition to increase in the supply of food quantity due to an increase in seaweed biomass, changes in host plant phenology and accompanying plant chemicals also caused patchiness in the quantity and quality of available food for phytal herbivores (Zimmerman *et al.* 1979, Bell *et al.* 1984, Steinberg 1984, Pavia and Åberg 1996). This in turn regulated epiphytic faunal numbers and diversity. Intraspecific and intraplant variations in feeding preference of herbivores on macroalgae have been demonstrated (Janzen 1979, Steinberg 1992, Poore 1994, Pennings *et al.* 1996). This was in part, attributed to the intraplant differences in the concentration of anti-herbivory secondary metabolites (Poore 1994, Cronina and Hay 1996, Pavia and Åberg 1996, Pavia *et al.* 2002, Macaya *et al.* 2005, Toth *et al.* 2005); or in part, due to differences in the nutrient levels among different plant parts. Secondary metabolite compounds were found to be most abundant in young, actively growing, and thus most productive seaweed portions. Newest plant portions are thus better defended than older portions. Species with apical growth, such as *Sargassum* spp., usually have highest concentrations of these metabolites in the upper portions of their branches (Philips and Towers 1982, Hay *et al.* 1988, Paul and Van Alstyne 1988, Pennings *et al.* 1996). Basal parts were also defended in *Sargassum filipendula* (Taylor *et al.* 2002) and *Ascophyllum nodosum* (Pavia *et al.* 2002, Toth *et al.* 2005). Tuomi *et al.* (1989) reported the anti-herbivory compound, phenols, accumulating

especially in vegetative apical parts of *Fucus vesiculosus*. Macaya *et al.* (2005) illustrated that apical (growth region) and basal parts (near the holdfast region) of brown macroalgae *Glossophora kunthii* and *Macrocystis integrifolia* in Chile were chemically defended against herbivores. Pavia *et al.* (1999) displayed the pronounced preference of adult isopod *Idotea granulosa* for meristematic apices of the brown alga *Ascophyllum nodosum*. This was probably due to the presence of higher nutrient content of the younger apices over older parts, despite the higher concentrations of phlorotannins in the meristematic apices (Pedersen 1984, Pavia *et al.* 1997). However, epiphytic fauna might prefer algae with lower nutritional values but with high anti-herbivory compounds that were able to provide the best protection and living sites over those with higher nutrition (Buschmann 1990, Duffy and Hay 1994, Kraufvelin *et al.* 2006). Holmlund *et al.* (1990) stated that phytal amphipods can tolerate and select host algae of high secondary metabolites to deter predation by the omnivorous fishes. Therefore, in the current study, the abundant herbivorous species found in the macroalgal lower zone might be able to tolerate and live in lower zone, despite the probably high content of secondary metabolites present in basal parts of the seaweed. Moreover, the more sedentary amphipods, such as caprellidean, develop specialized morphological and behavioral attributes that correspond to the types of habitats in which they occur (Hagerman 1966, Fenwick

1976, Caine 1978, Steele 1988). They cling themselves firmly on the holdfast as well as branches in the lower zone.

Other benthos like tubeworms, barnacles and bivalves in the present investigation required more surface area for attachment. This was provided by greater seaweed biomass in the lower zone. There were findings that abundance of some sessile organisms in an epiphytic faunal community increased when the structural complexity of the substratum was experimentally increased (Russ 1980) due to the consequential enhancement of colonisable surface areas (Lippert *et al.* 2001). This facilitated the settlement and growth of sessile organisms. Furthermore, fouling was singularly rapid during the times of algal dieback as the levels of anti-fouling chemicals were lower when the macroalgae decayed (Hay *et al.* 1988, Hay 1996). Brachyurans and macrurans were wholly associated with lower zone of the algae since the abundance of invertebrates was high. They can thus prey on other invertebrates.

Fish juveniles of *Sebastiscus marmoratus* and *Petrocrites breviceps*, lophogasters, harpacticoids and calanoid copepods were frequently associated with middle and upper zones of *Sargassum siliquastrum*. These were fauna with pelagic components

and with higher mobility. Mobile phytal animals, such as hyperiidean amphipods and lophogasters, were observed to undergo transition from one patch of algae to another over a range of habitat types (Gunnill 1982b, Liu and Wang 2000). Harpacticoid copepods are good swimmers, in particular the phytal ones (Moore 1973, Hicks 1977, Hicks 1985, Palmer 1988). Therefore, faunas associated with the middle and upper zones of *Sargassum siliquastrum* were relatively more mobile and among-plant transition was speculated. Besides, fauna might develop features and adaptations to be associated with a particular habitat. Schmidt and Scheibling (2007) indicated that selection of algal habitats by mobile macrofauna was likely determined by the different shelter and foraging opportunities offered by macroalgal communities of dissimilar morphologies. Shrimps living on pelagic *Sargassum* have body shapes and colouration matching the parts of the host plant on which they lived, which presumably helped to camouflage them from fish predators (Hacker and Madin 1991). Jenkins and Sutherland (1997) stated that the close association of pipefish *Stigmatopora* spp. in the narrow-leaf seagrass habitat but not in broad-leaf seagrass bed was attributable to the strong mimic of the fish with the eelgrass having long and narrow body shape and olive green pigmentation as well as synchronized movement in the current (Howard and Koehn 1985). This close mimicry might be applicable to the fish *Petrocrites breviceps* juveniles, having slender body and brown pigmentation

(Sadovy and Cornish 2000) that move in harmonized motion with the seaweed (per. obs.). They were found to reside in the upper zone along with the narrower fronds of *Sargassum siliquastrum* in the present study. The present data exhibited that gammaridean amphipods and their juveniles were occasionally located in middle and upper zones. *Sargassum* spp., the apical-growing macroalgae, usually had highest concentrations of secondary metabolites in the upper portions of their branches (Philips and Towers 1982, Hay *et al.* 1988, Paul and Van Alstyne 1988, Pennings *et al.* 1996). Reproductive tissues might also be differentially defended by allocating more phlorotannin to reproductive parts than to vegetative blades, making the reproductive structures less vulnerable to herbivore consumers (Steinberg 1984). Therefore, the occasional appearance of gammarideans in seaweed upper zone might probably be related simply to possible movement along the three zones within an individual plant by the relatively mobile amphipods but not to feeding preference on the upper portion that consists of apical growing tissues and reproductive parts. However, previous studies showed that for some herbivores, feeding preference can be concentrated on young tissues (Cronin and Hay 1996, Taylor *et al.* 2002). Apical parts of brown seaweed *Ascophyllum nodosum* fronds were selected as food on the basis of chemical and/or structural characteristics, as the toughness, secondary compounds and/or quality as food vary along algal shoots (Poore 1994, Pavia and

Åberg 1996, Viejo and Åberg 2003). As a result, some gammarideans resided in the upper zone might prefer to feed on young tissues of more tender texture than the tough older parts in the lower zone (Taylor *et al.* 2002).

5.5 Summary and Conclusion

In this study, the increase in the physical properties of *Sargassum siliquastrum* generally produced concomitant increase in the abundance and diversity of the associated faunal community. The macroalgal biomass, expressed as fresh weight, provided greater effects on epiphytic faunal abundance and species richness, particularly during seaweed reproductive and dieback stages, when compared with other components of structural complexity. The provision of affluent food source (i.e. host plant tissue, epiphytic plant and phytodetritus), enhanced surface area for attachment and protection, as well as amelioration of the strong hydrodynamics, were probably the factors that lead to the augmentation of faunal numbers and species diversity by an increase of seaweed biomass. In terms of structural complexity alone, seaweed branch number imposed a relatively more influential positive effect on epiphytic faunal abundance and species richness, especially during times of seaweed rapid growth and reproduction, when compared with seaweed length. The increase in

faunal abundance and species richness with increase in branch number might be attributable to an increase in habitable space between the branches for the fauna to attach and stay away from predation.

Within-plant zonation pattern was more pronounced in seaweed reproductive and dieback stages. Species richness and abundance were in the main the highest in lower zone of the algae, including the holdfast. This was possibly due to an increase in the surface area of the algae for faunal colonization and structural complexity for better protection from physical stress and predation, as a result of greater biomass of the lower zone. Specific faunas were observed to settle in particular zone of *Sargassum siliquastrum* based on association with specific environment parameters, e.g. in terms of food and shelter provision and differences in feeding mode, behavior and mobility. In general, faunas resided in the lower zone of *Sargassum siliquastrum* were more sedentary and mostly herbivorous or detritivorous; while faunas associated with middle or upper zone were more mobile.

On the whole, no one particular macroalgal physical parameter can be singled out as the determining factor in controlling the observed epiphytic faunal composition. It is preliminarily believed that food availability, and not predation pressure, was the

limiting factor. This is supported by the findings in the present study, both with respect to the structural complexity of the algal plant and within-plant zonation, that the associated epiphytic faunal assemblage was more dependent on the availability of macroalgal biomass than on any of the other parameters considered.

Table 5.1 Mean (± S.D.) seaweed length (cm) of each size class during each seaweed growth stage in the study sites LLT and LFN. S=small-sized, M=medium-sized and L=large-sized classes.

Seaweed Growth Stage	Size Class	LLT	LFN
06 Rapid Growth	S	31.6±7.2	/
	M	78.5±12.1	/
	L	133.7±7.1	/
06 Reproductive	S	59.2±33.2	58.1±21.7
	M	130.8±12.9	141.0±50.2
	L	195.6±28.8	173.5±57.6
07 Dieback	S	40.0±7.1	74.0±4.2
	M	111.0±8.5	107.5±2.1
	L	196.5±13.4	148.5±4.9
07 Rapid Growth	S	54.7±26.7	28.5±5.5
	M	109.2±25.8	62.7±13.8
	L	149.2±58.8	107.9±40.0
07 Reproductive	S	60.0±21.2	71.5±13.9
	M	164.5±21.9	133.3±15.1
	L	233.0±5.7	190.3±14.4
08 Dieback	S	16.4±13.7	49.0±15.6
	M	88.1±7.6	77.5±17.7
	L	187.2±46.7	108.0±11.3

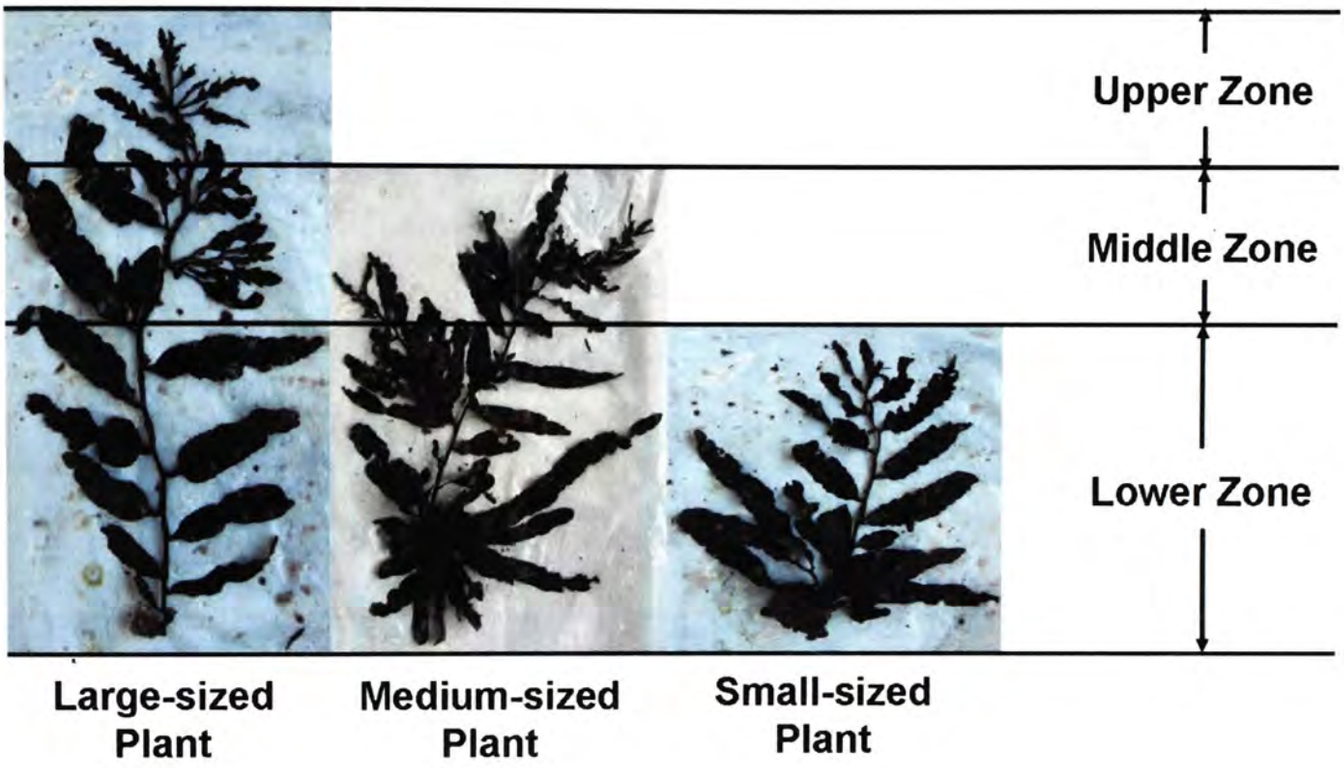


Fig. 5.1 Designation of within-plant zonation of *Sargassum siliquastrum* in the experiment. The size of the small-sized plants in each growth stage was used as the basis to determine the lower zone of the vegetation, that of the medium-sized plants, the middle zone. The upper zone was that part of the large-sized plant above the height of the medium-sized plants.

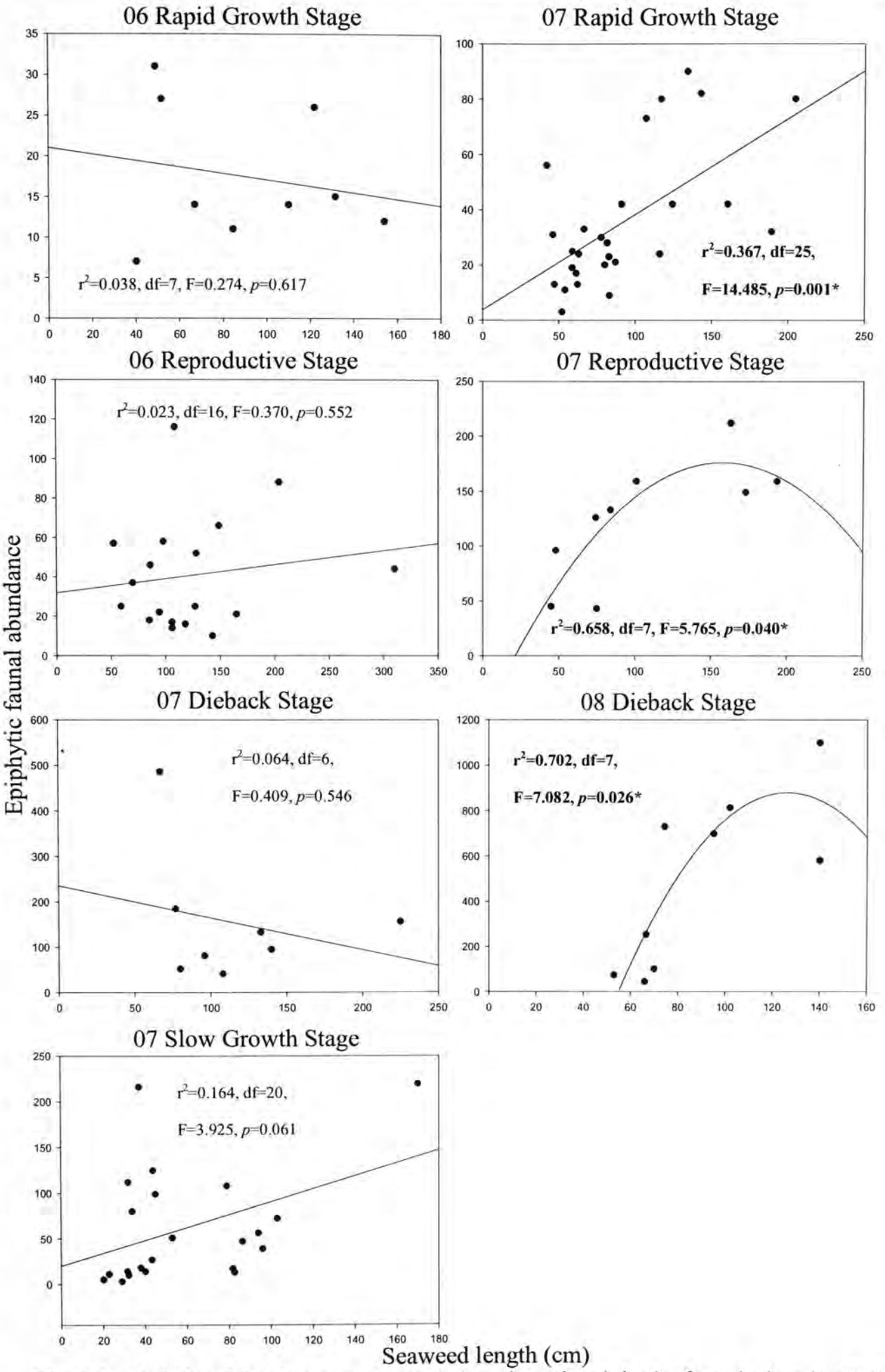


Fig. 5.2 Relationship between seaweed length and epiphytic faunal abundance in each growth stage at LLT. Regression analyses indicate relationships in 07 Rapid Growth, 07 Reproductive and 08 Dieback stages to be statistically significant (marked in bold with *). Regression equations not shown.

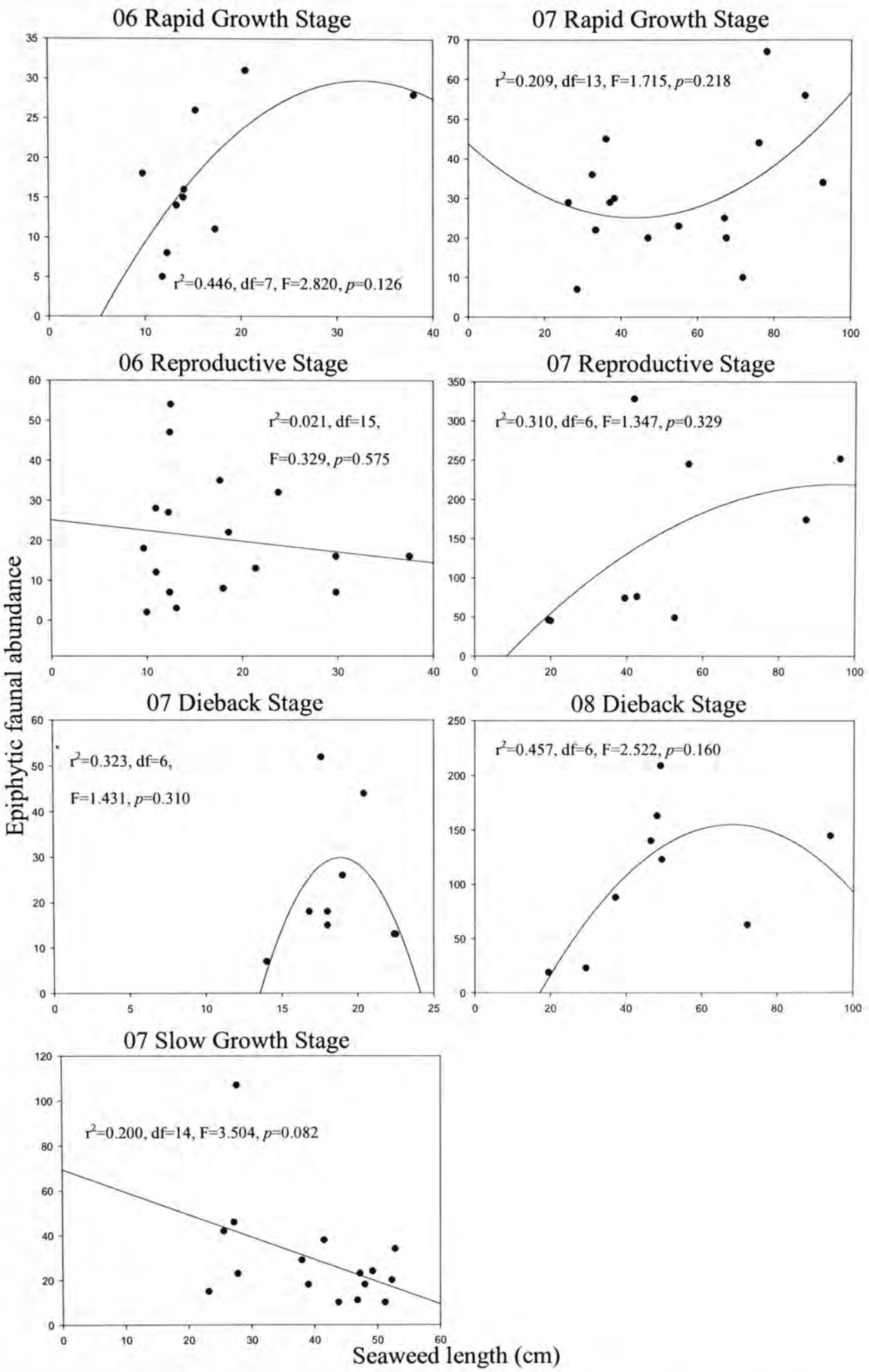


Fig. 5.3 Relationship between seaweed length and epiphytic faunal abundance in each growth stage at LLS. Regression analyses indicate all relationships to be not statistically significant. Regression equations not shown.

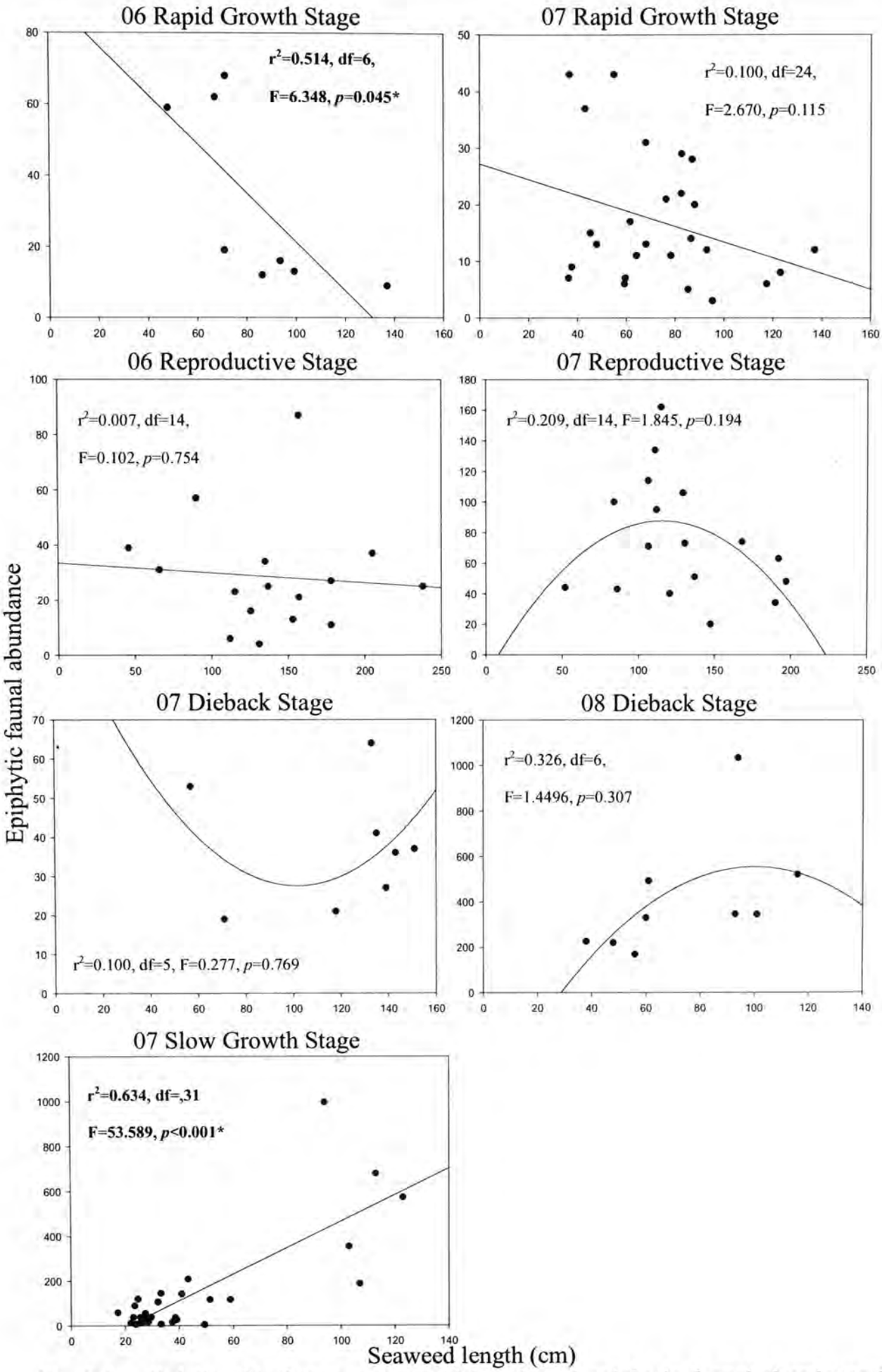


Fig. 5.4 Relationship between seaweed length and epiphytic faunal abundance in each growth stage at LFN. Regression analyses indicate relationships in 06 Rapid Growth and 07 Slow Growth stages to be statistically significant (marked in bold with *). Regression equations not shown.

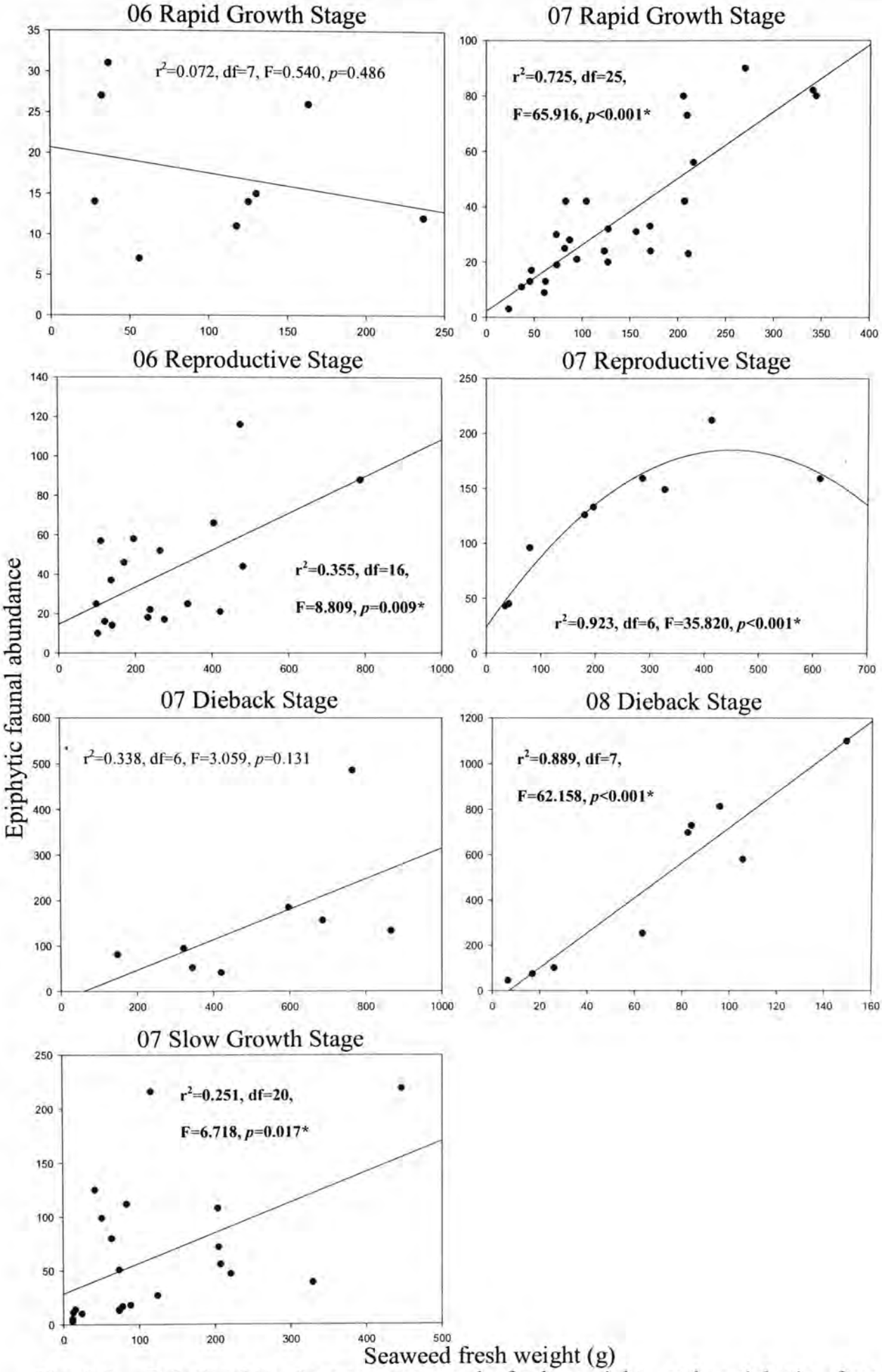


Fig. 5.5 Relationship between seaweed fresh weight and epiphytic faunal abundance in each growth stage at LLT. Regression analyses indicate all relationships except in 06 Rapid Growth and 07 Dieback stages to be statistically significant (marked in bold with *). Regression equations not shown.

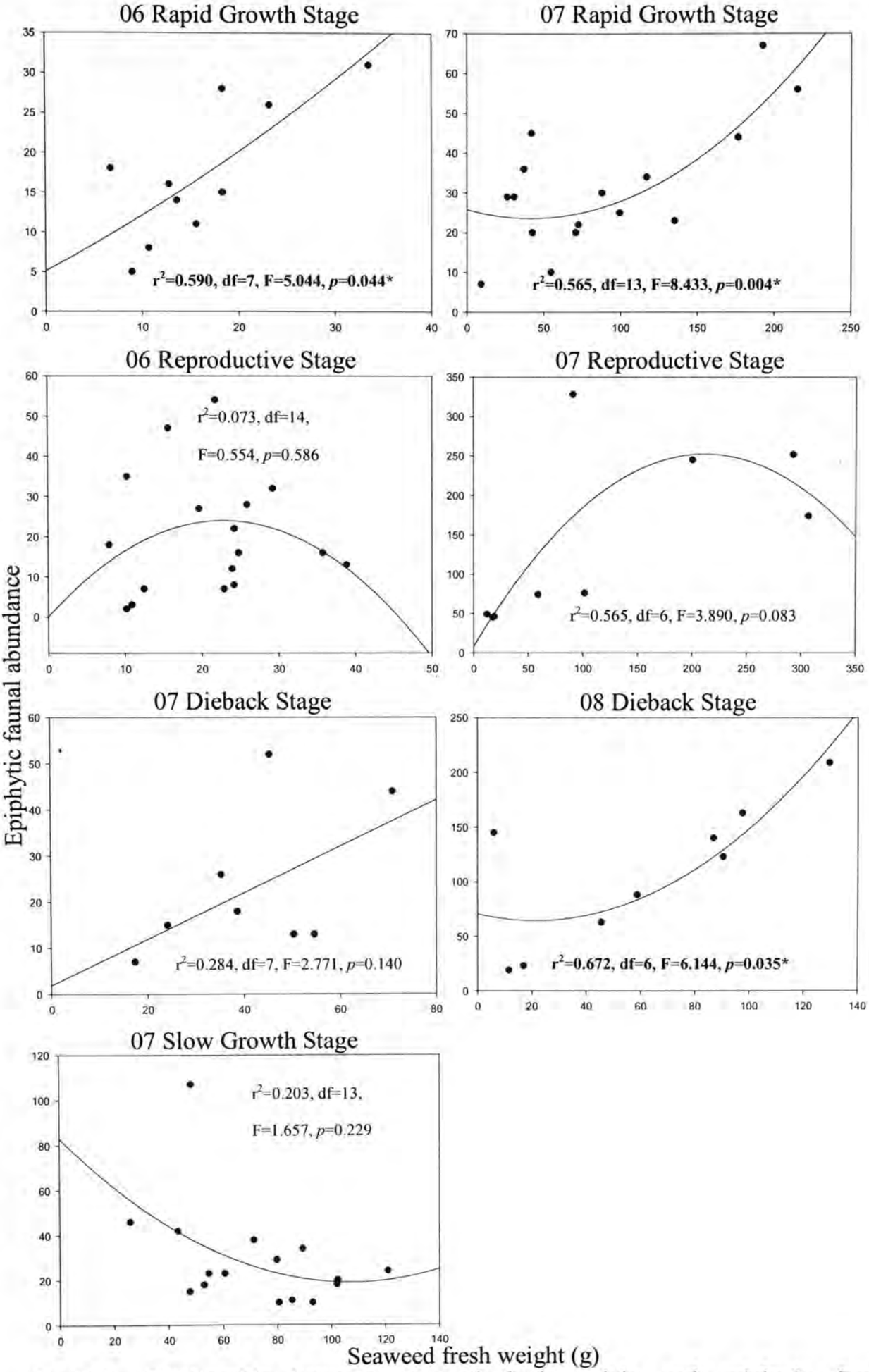


Fig. 5.6 Relationship between seaweed fresh weight and epiphytic faunal abundance in each growth stage at LLS. Regression analyses indicate relationships in 06 Rapid Growth, 07 Rapid Growth and 08 Dieback stages to be statistically significant (marked in bold with *). Regression equations not shown.

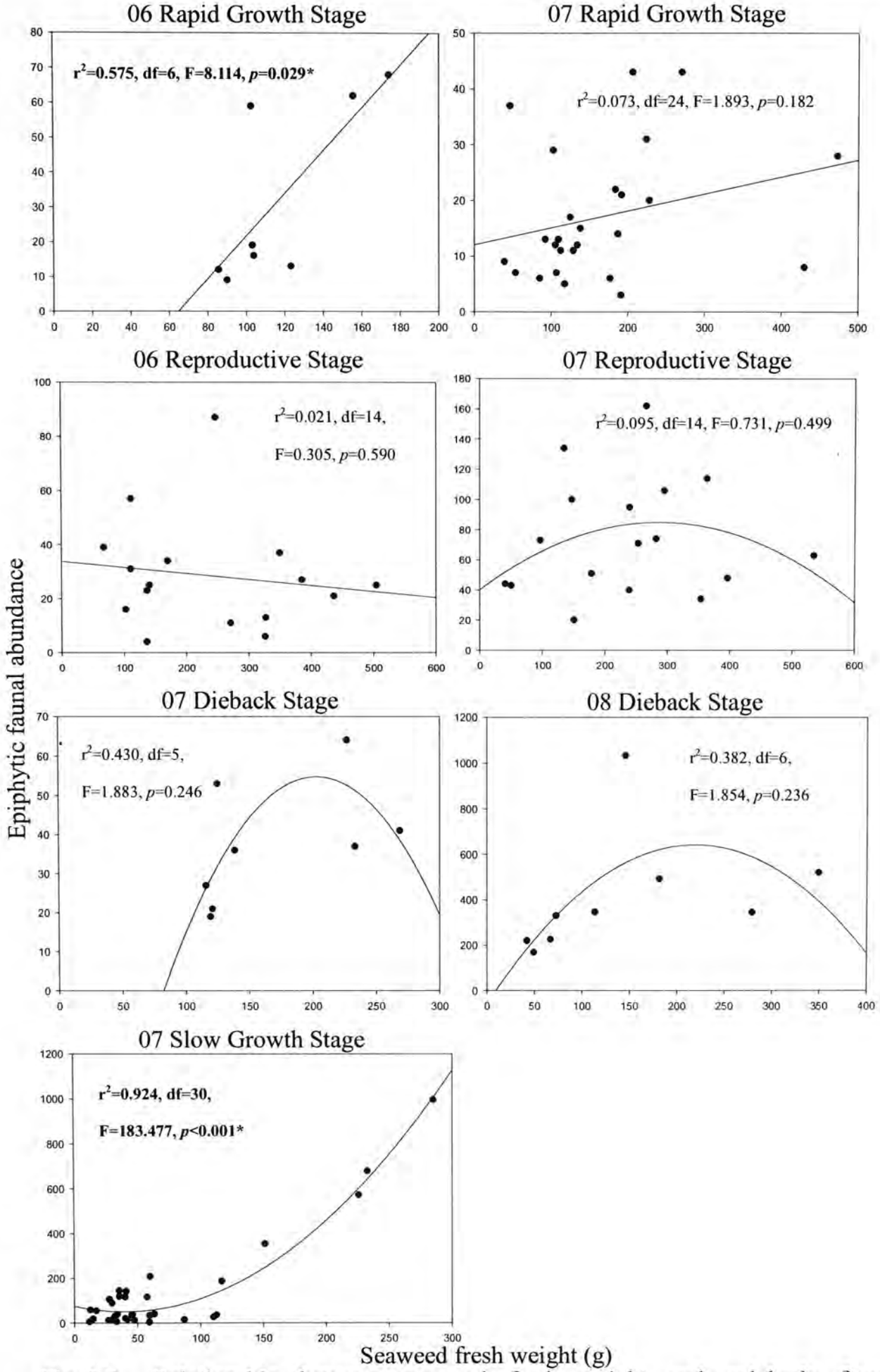


Fig. 5.7 Relationship between seaweed fresh weight and epiphytic faunal abundance in each growth stage at LFN. Regression analyses indicate relationships in 06 Rapid Growth and 07 Slow Growth stages to be statistically significant (marked in bold with *). Regression equations not shown.

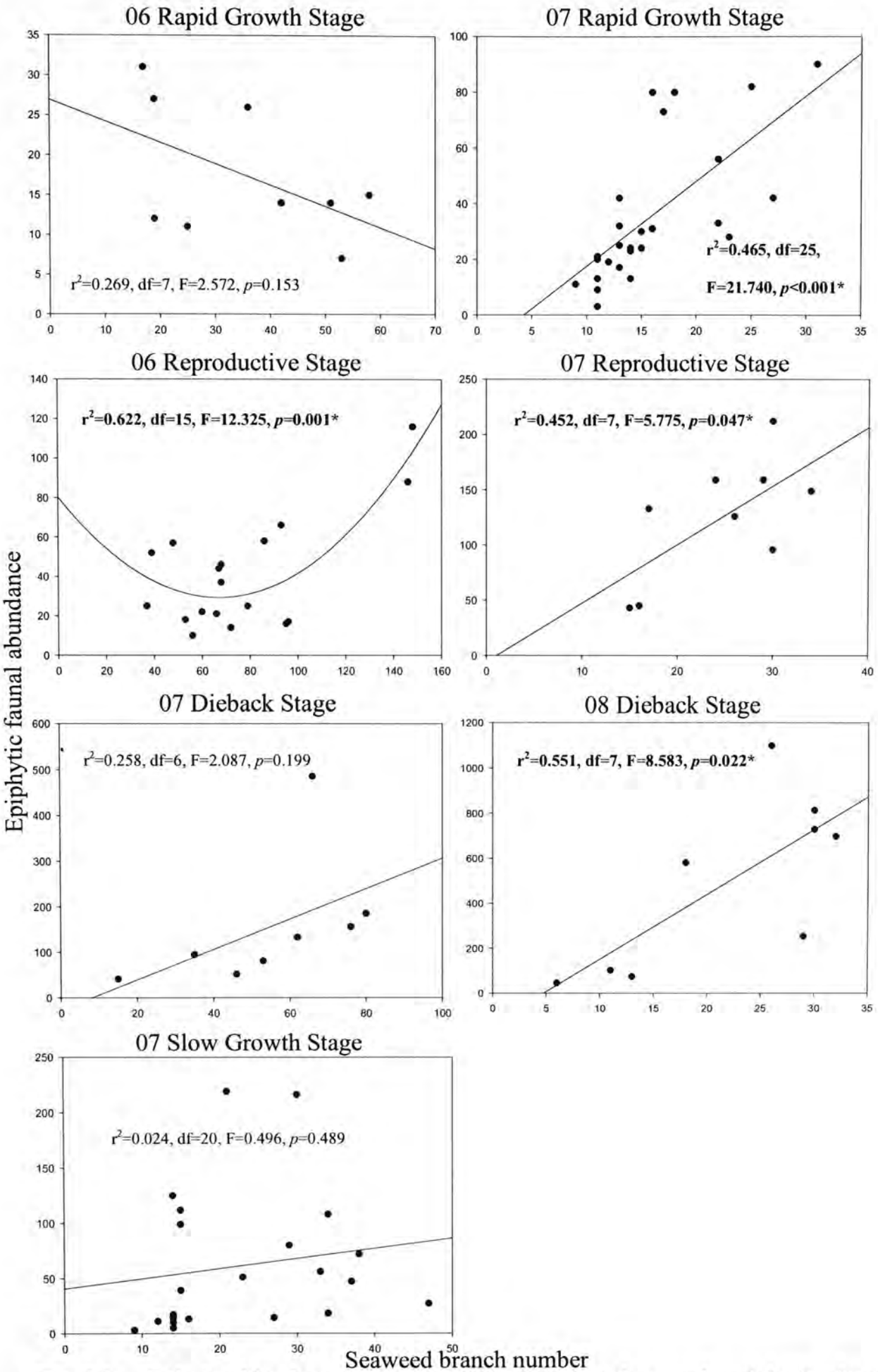


Fig. 5.8 Relationship between seaweed branch number and epiphytic faunal abundance in each growth stage at LLT. Regression analyses indicate relationships in 06 Reproductive, 07 Rapid Growth, 07 Reproductive and 08 Dieback stages to be statistically significant (marked in bold with *). Regression equations not shown.

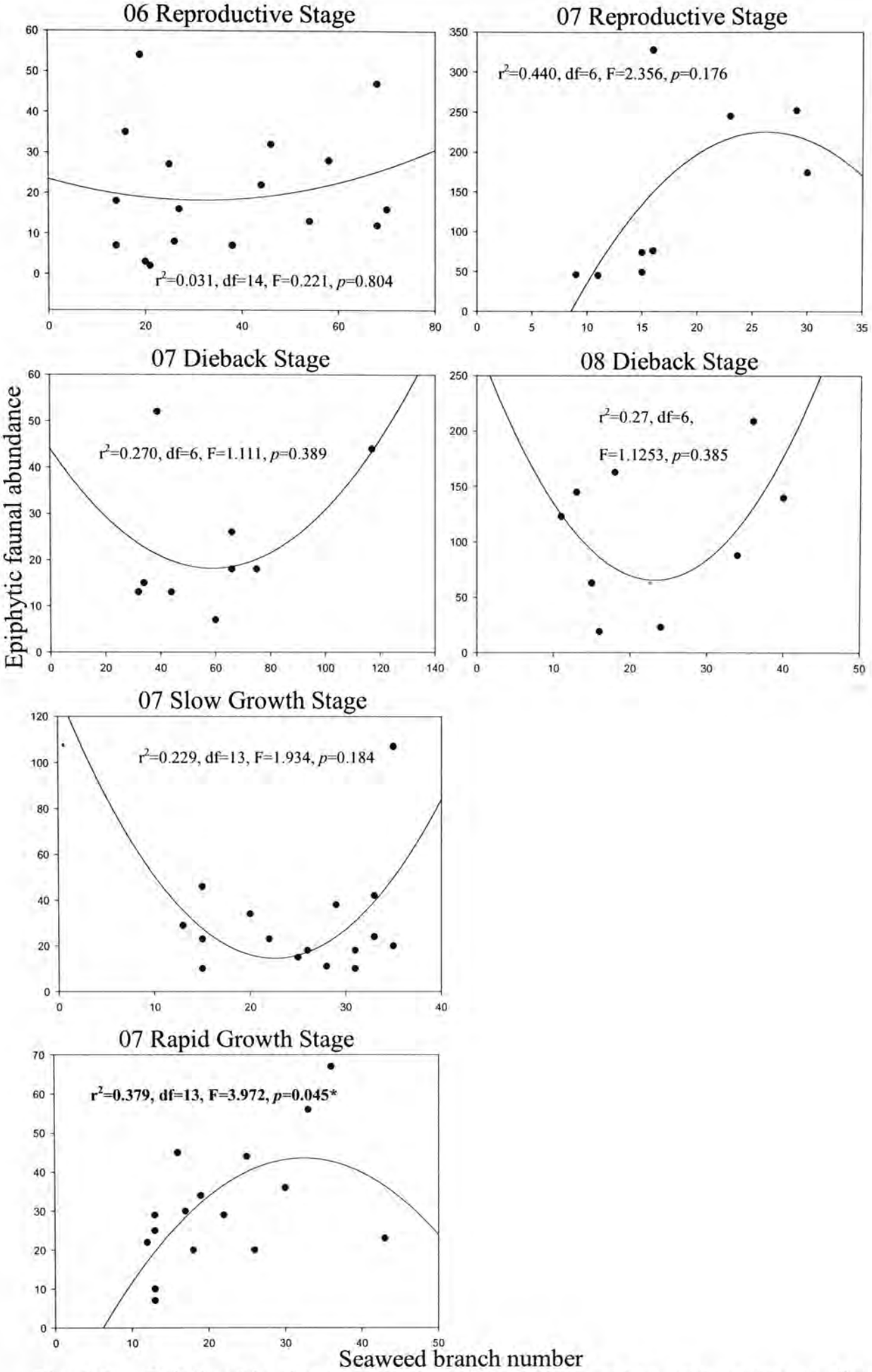


Fig. 5.9 Relationship between seaweed branch number and epiphytic faunal abundance in each growth stage at LLS. Regression analyses indicate relationship in 07 Rapid Growth stage to be statistically significant (marked in bold with *). Regression equations not shown.

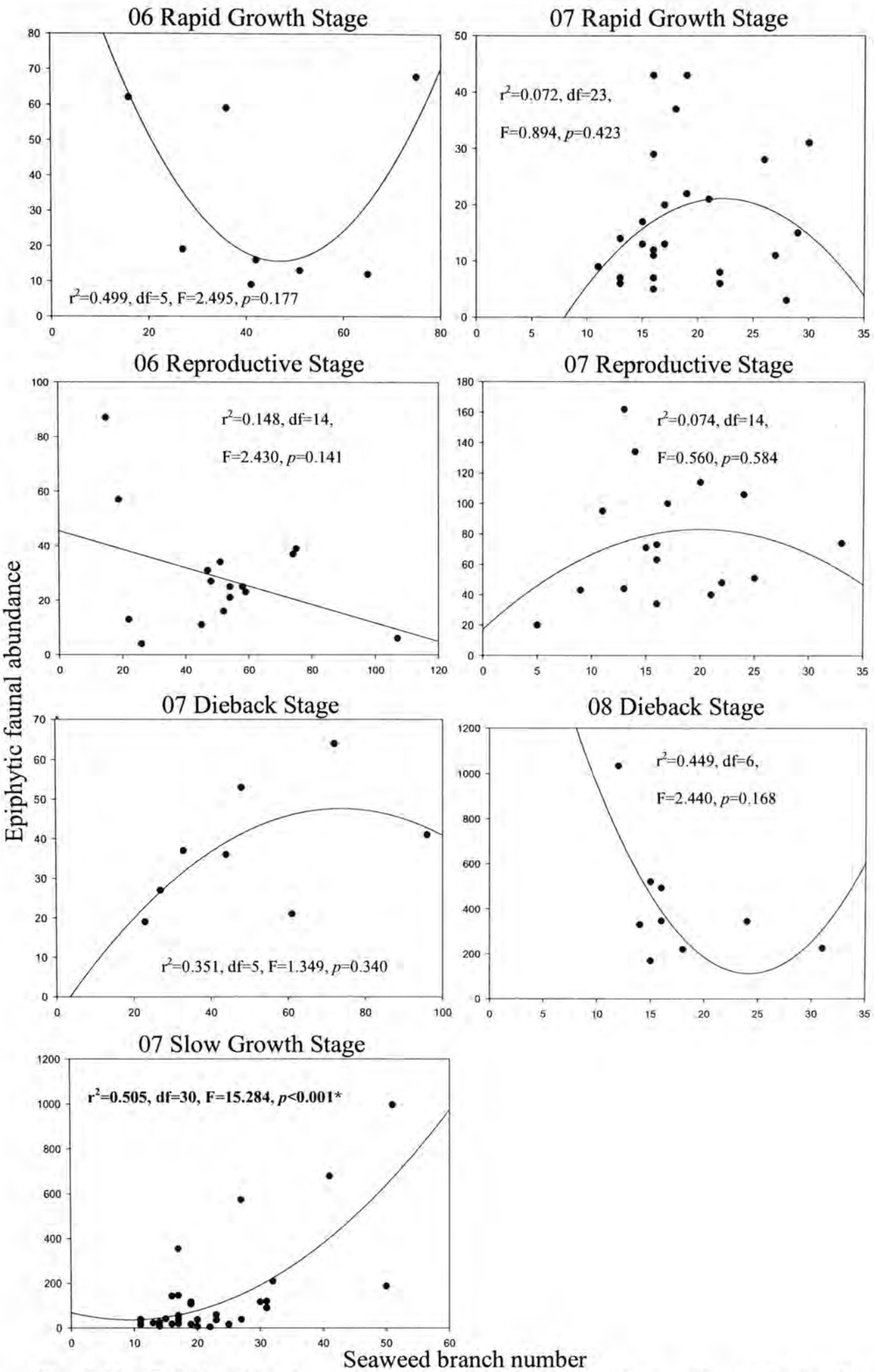


Fig. 5.10 Relationship between seaweed branch number and epiphytic faunal abundance in each growth stage at LFN. Regression analyses indicate relationship in 07 Slow Growth stage to be statistically significant (marked in bold with *). Regression equations not shown.

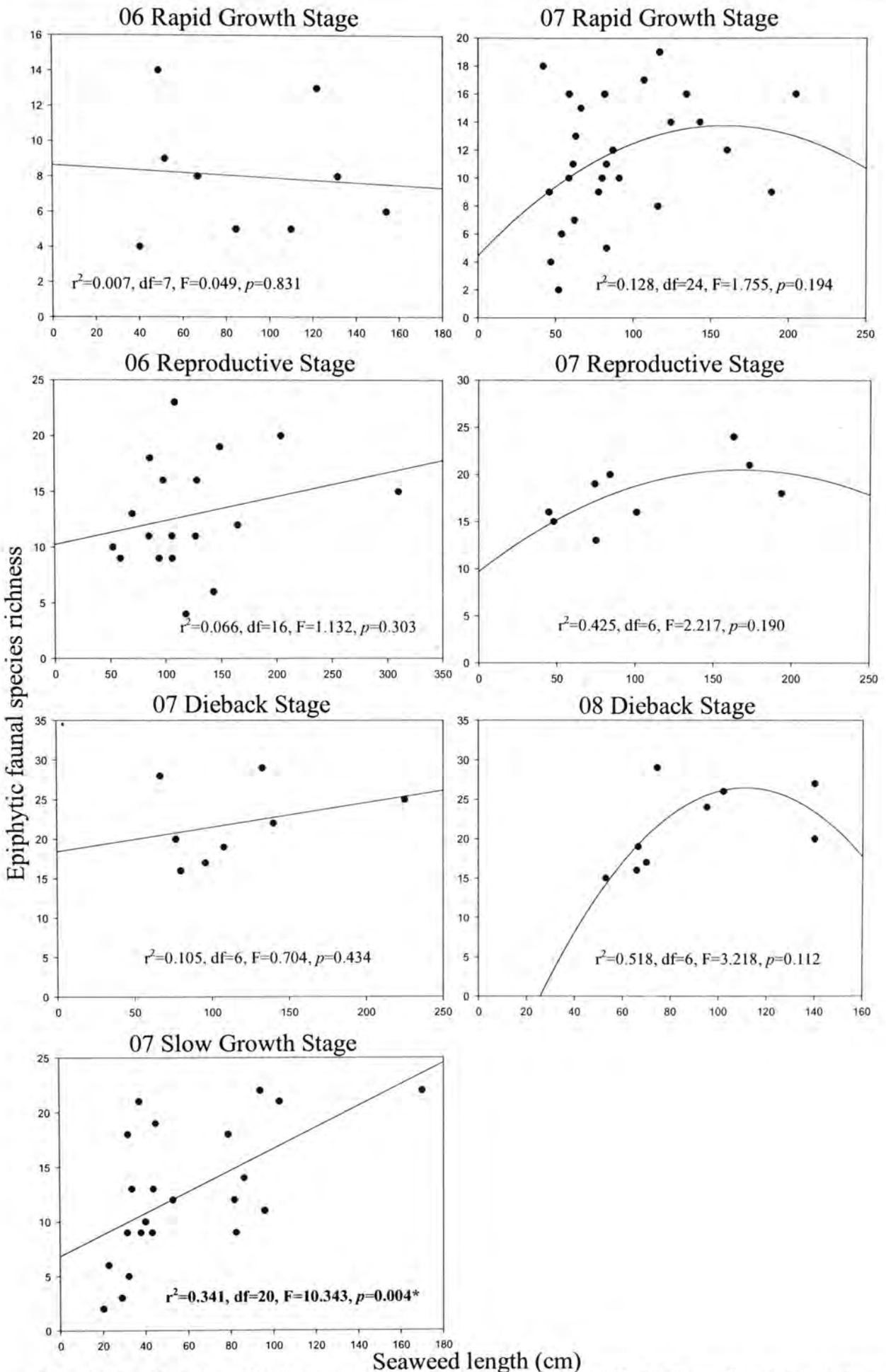


Fig. 5.11 Relationship between seaweed length and epiphytic faunal species richness in each growth stage at LLT. Regression analyses indicate relationship in 07 Slow Growth stage to be statistically significant (marked in bold with *). Regression equations not shown.

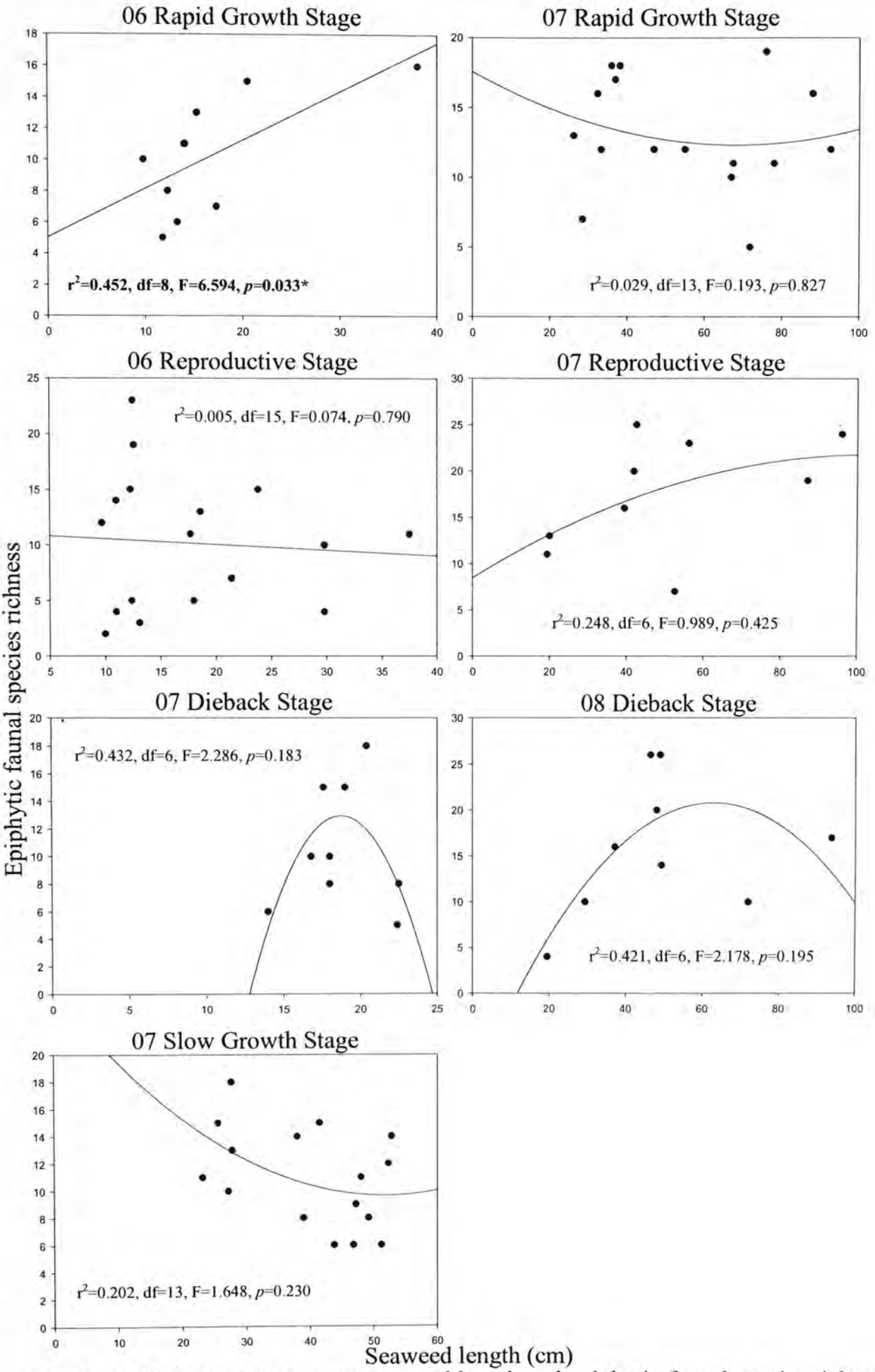


Fig. 5.12 Relationship between seaweed length and epiphytic faunal species richness in each growth stage at LLS. Regression analyses indicate relationship in 06 Rapid Growth stage to be statistically significant (marked in bold with *). Regression equations not shown.

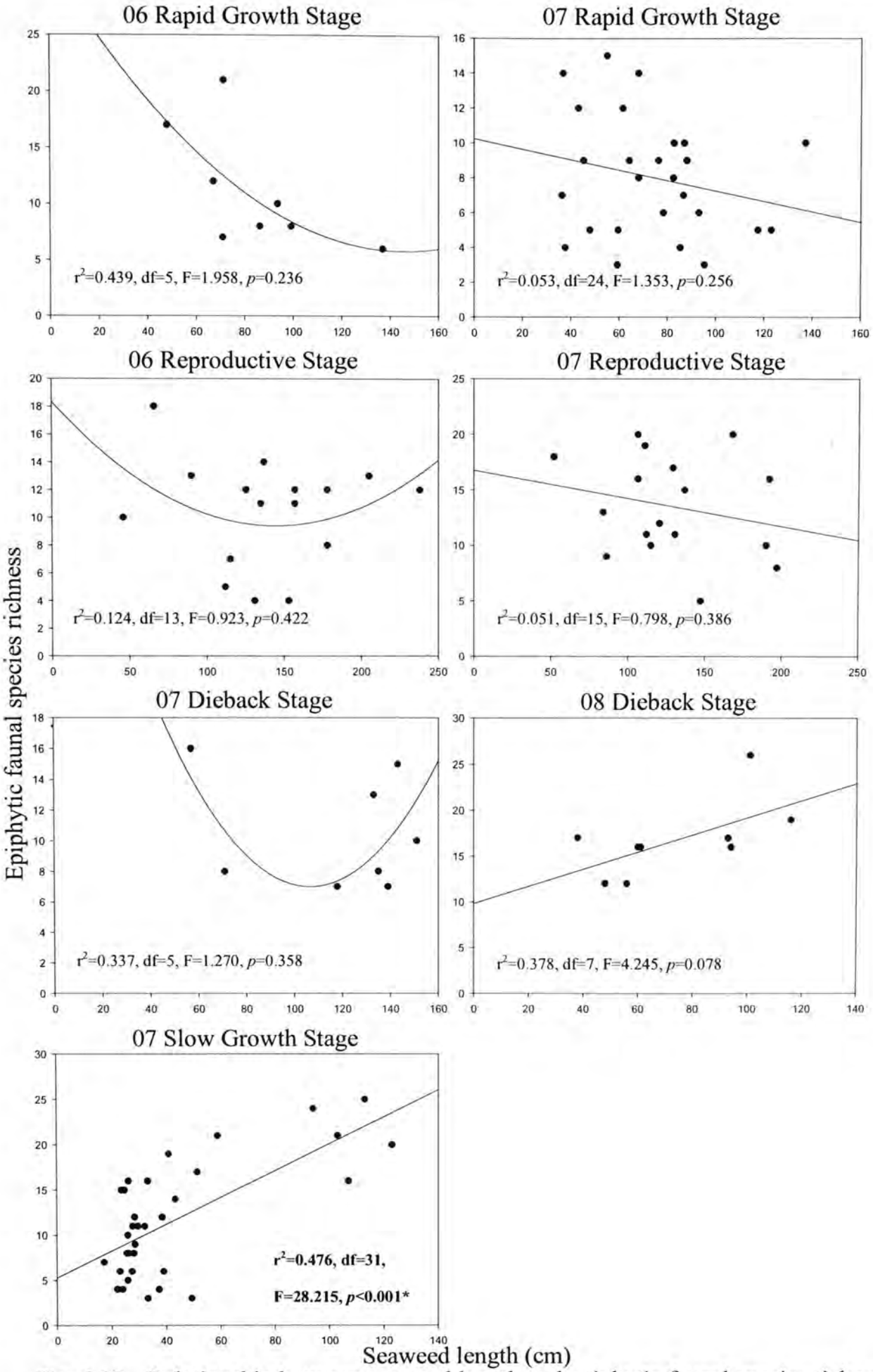


Fig. 5.13 Relationship between seaweed length and epiphytic faunal species richness in each growth stage at LFN. Regression analyses indicate relationship in 07 Rapid Growth stage to be statistically significant (marked in bold with *). Regression equations not shown.

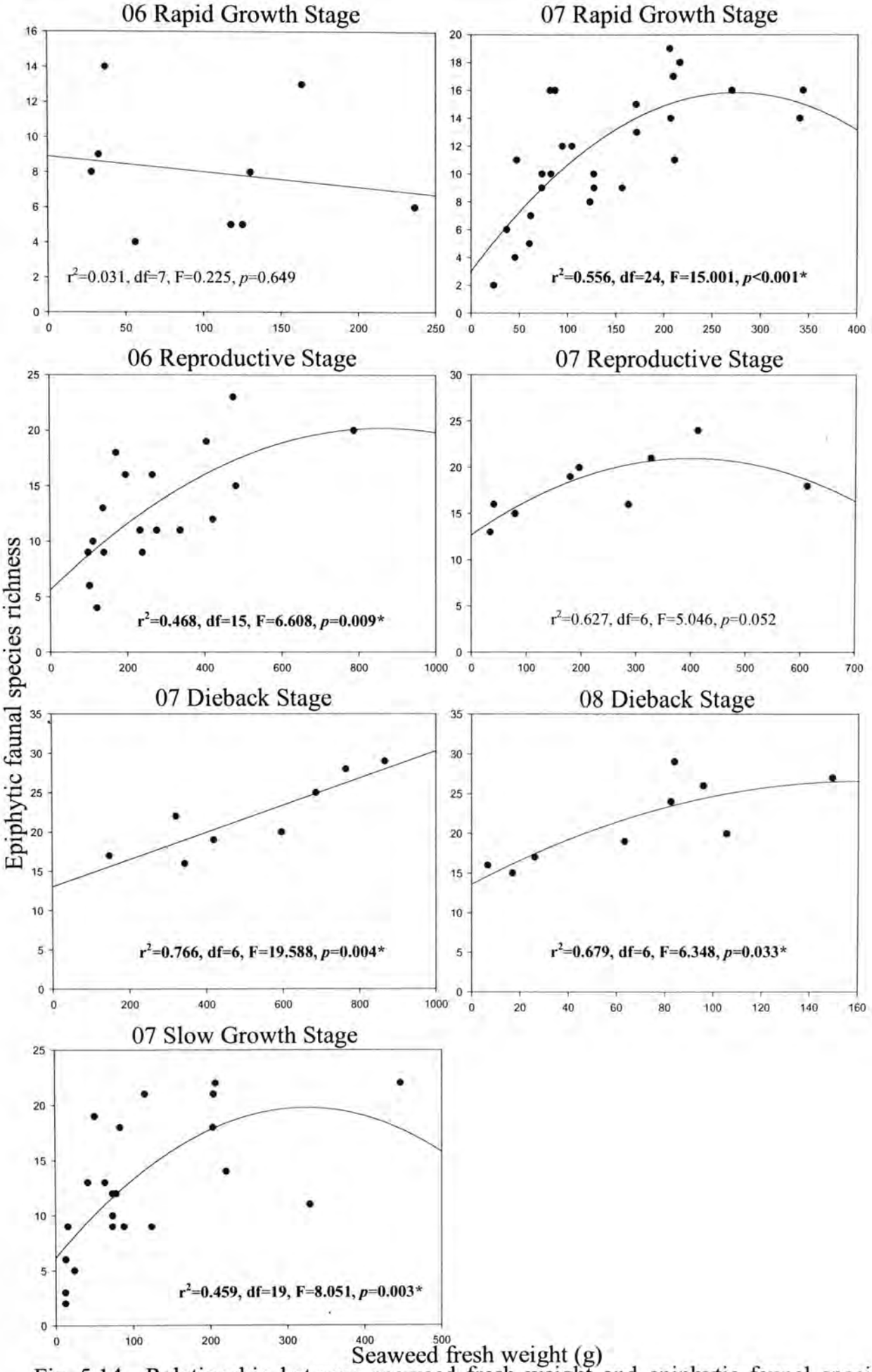


Fig. 5.14 Relationship between seaweed fresh weight and epiphytic faunal species richness in each growth stage at LLT. Regression analyses indicate all relationships except in 06 Rapid Growth and 07 Reproductive stages to be statistically significant (marked in bold with *). Regression equations not shown.

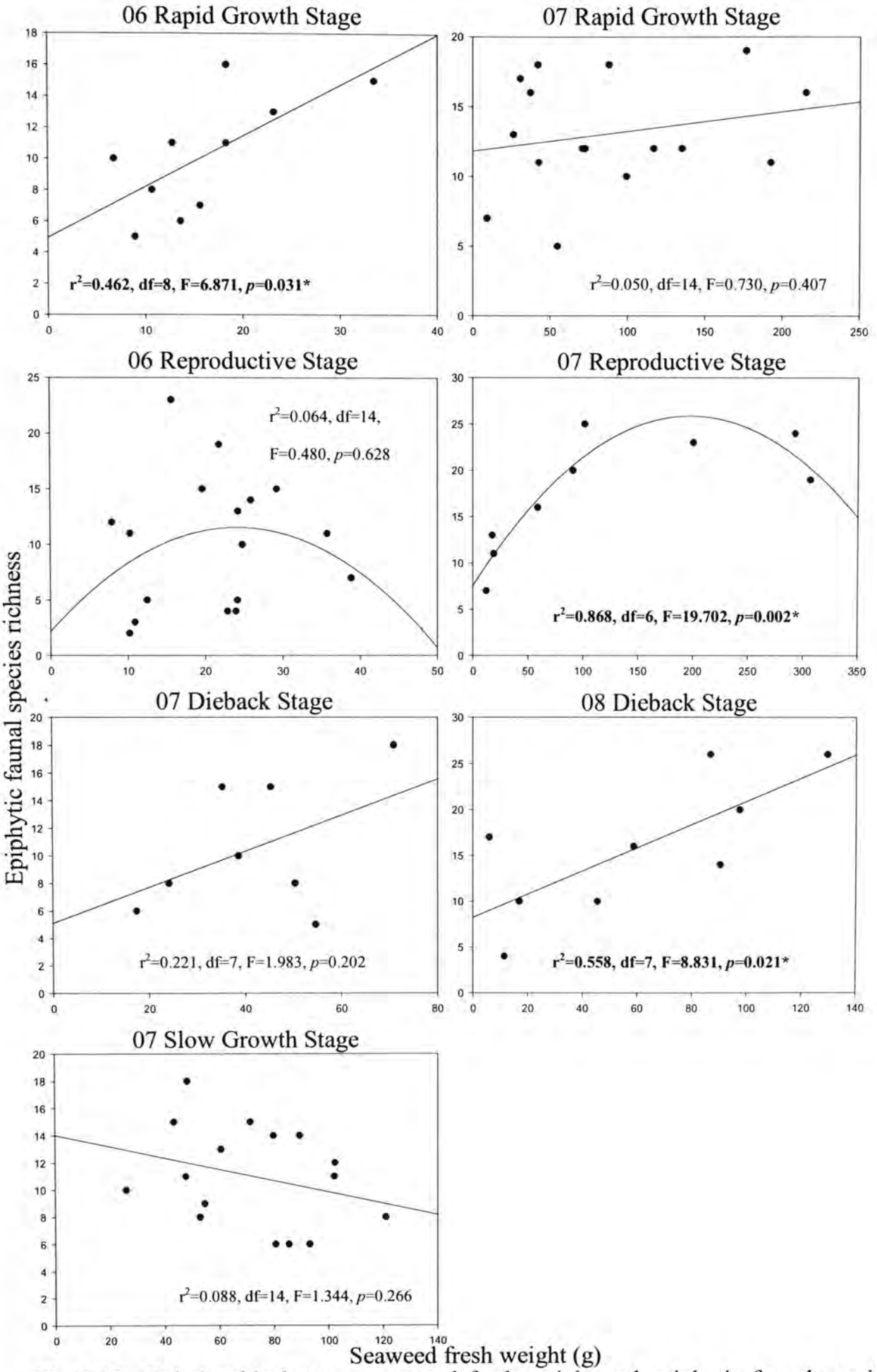


Fig. 5.15 Relationship between seaweed fresh weight and epiphytic faunal species richness in each growth stage at LLS. Regression analyses indicate relationships in 06 Rapid Growth, 07 Reproductive and 08 Dieback stages to be statistically significant (marked in bold with *). Regression equations not shown.

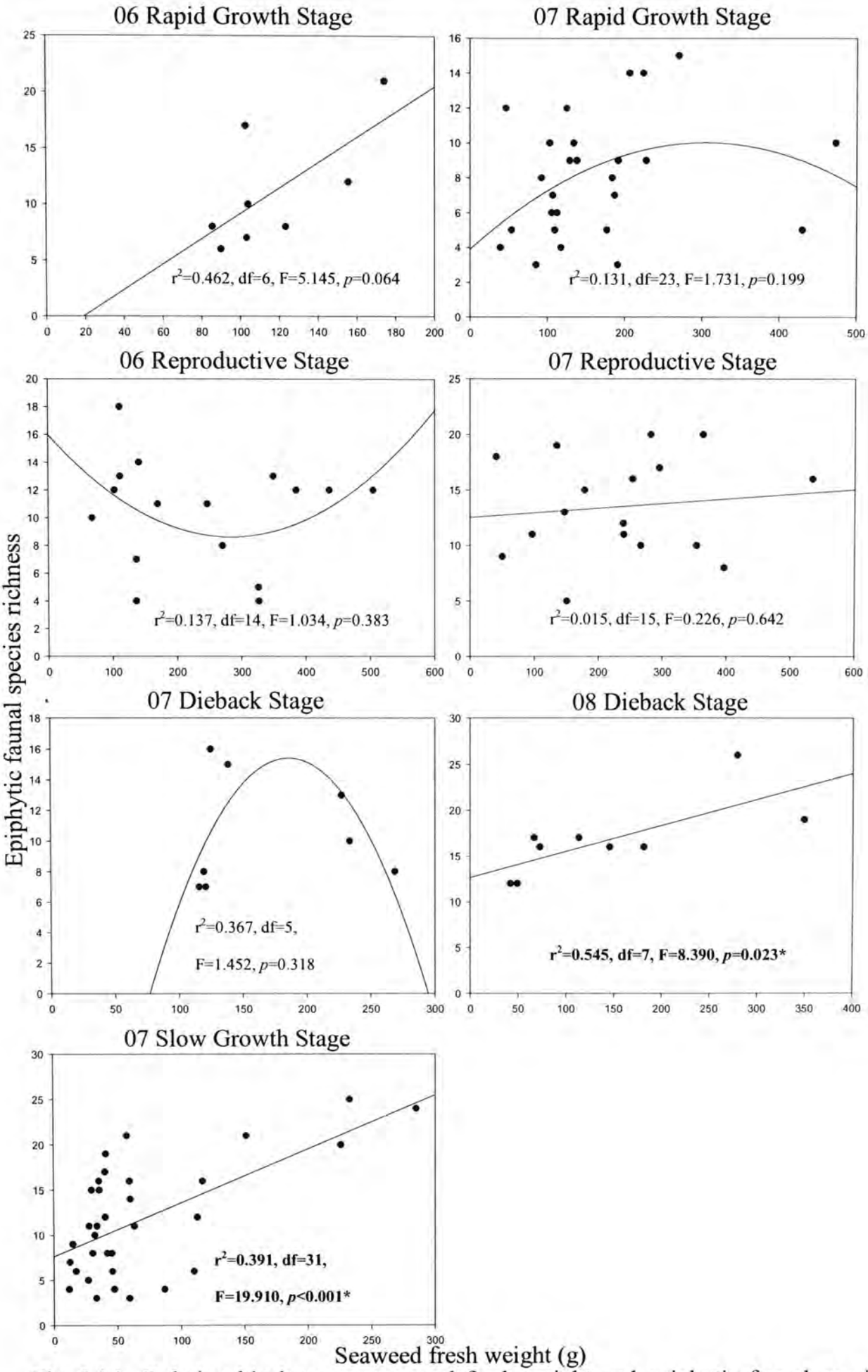


Fig. 5.16 Relationship between seaweed fresh weight and epiphytic faunal species richness in each growth stage at LFN. Regression analyses indicate relationships in 07 Slow Growth and 08 Dieback stages to be statistically significant (marked in bold with *). Regression equations not shown.

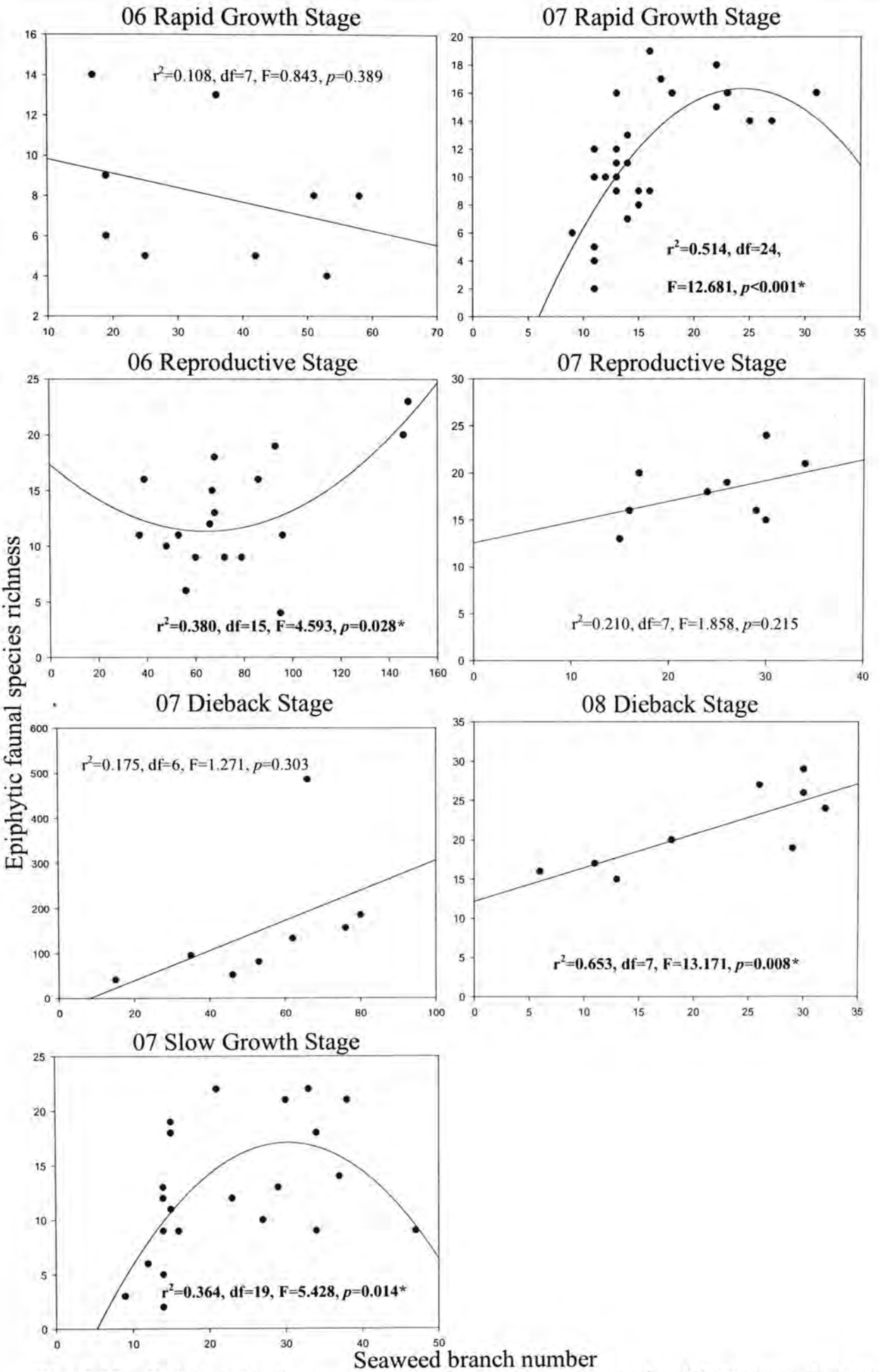


Fig. 5.17 Relationship between seaweed branch number and epiphytic faunal species richness in each growth stage at LLT. Regression analyses indicate relationships in 06 Reproductive, 07 Slow Growth, 07 Rapid Growth and 08 Dieback stages to be statistically significant (marked in bold with *). Regression equations not shown.

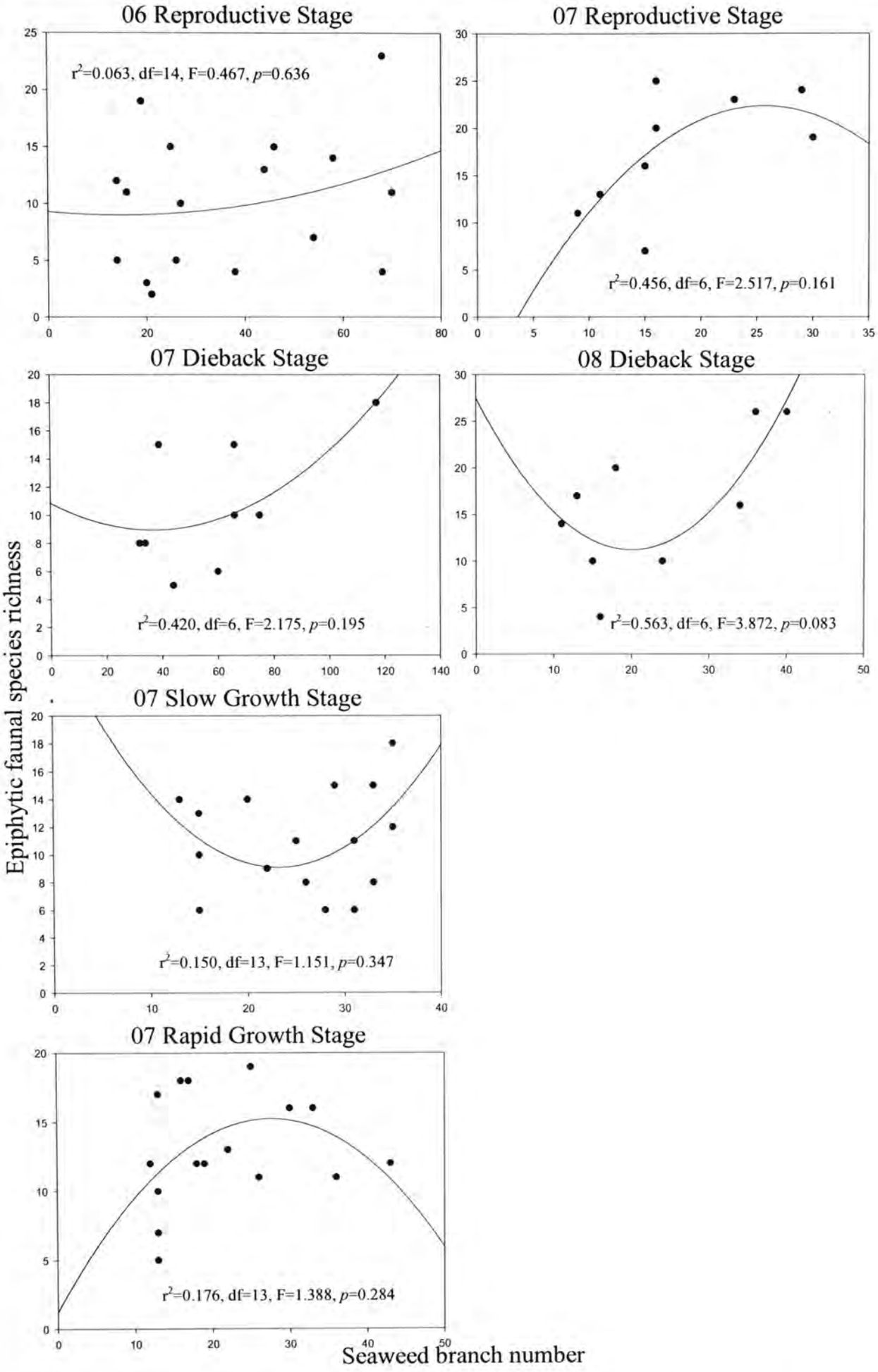


Fig. 5.18 Relationship between seaweed branch number and epiphytic faunal species richness in each growth stage at LLS. Regression analyses indicate all relationships to be not statistically significant. Regression equations not shown.

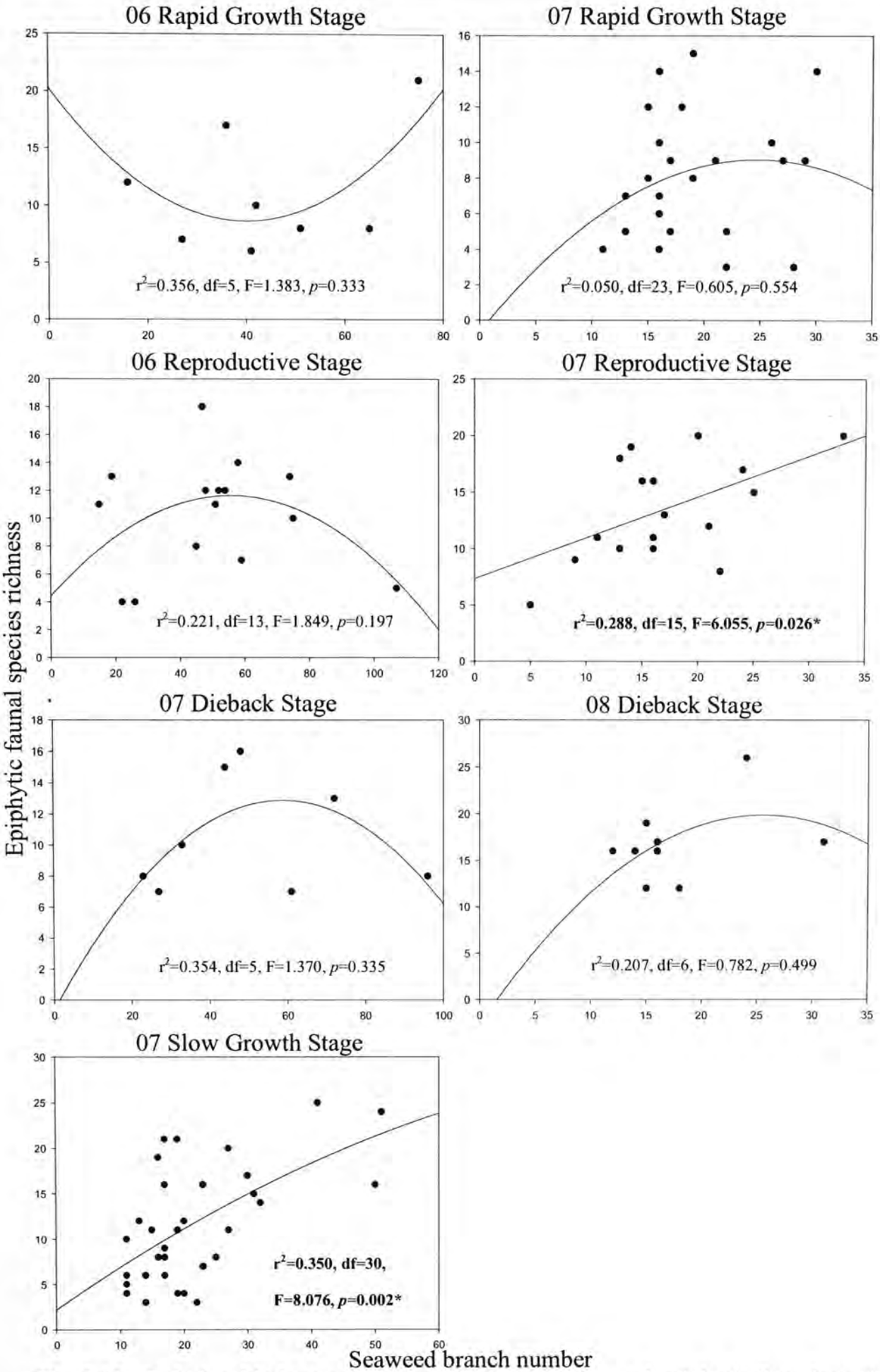


Fig. 5.19 Relationship between seaweed branch number and epiphytic faunal species richness in each growth stage at LFN. Regression analyses indicate relationships in 07 Slow Growth and 07 Reproductive stages to be statistically significant (marked in bold with *). Regression equations not shown.

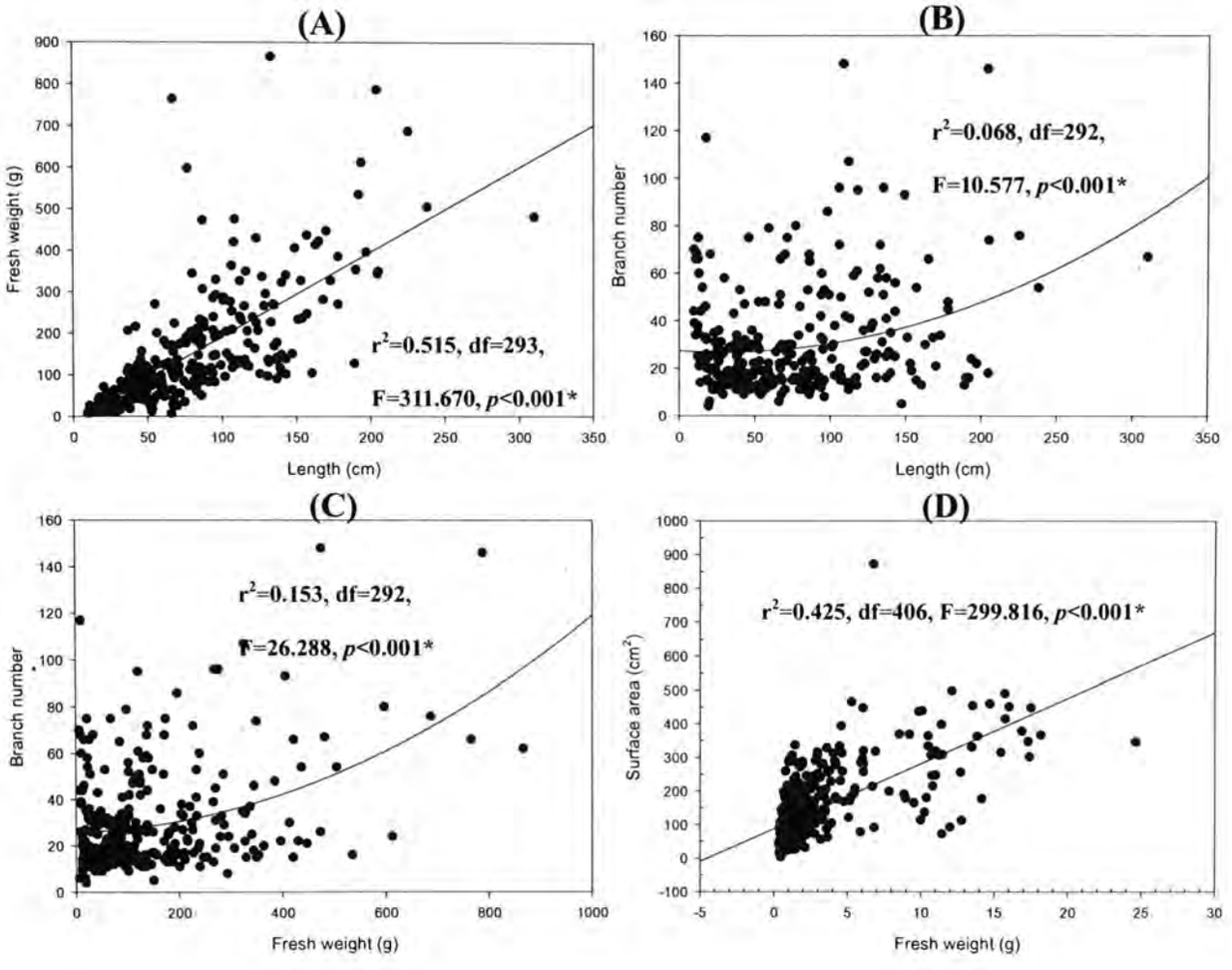


Fig. 5.20 Relationship between parameters: (**A**). fresh weight and length, (**B**). branch number and length, (**C**). branch number and fresh weight, (**D**). surface area and fresh weight, of *Sargassum siliquastrum* in both study sites. Regression analyses indicate all relationships to be statistically significant. Regression equations not shown.

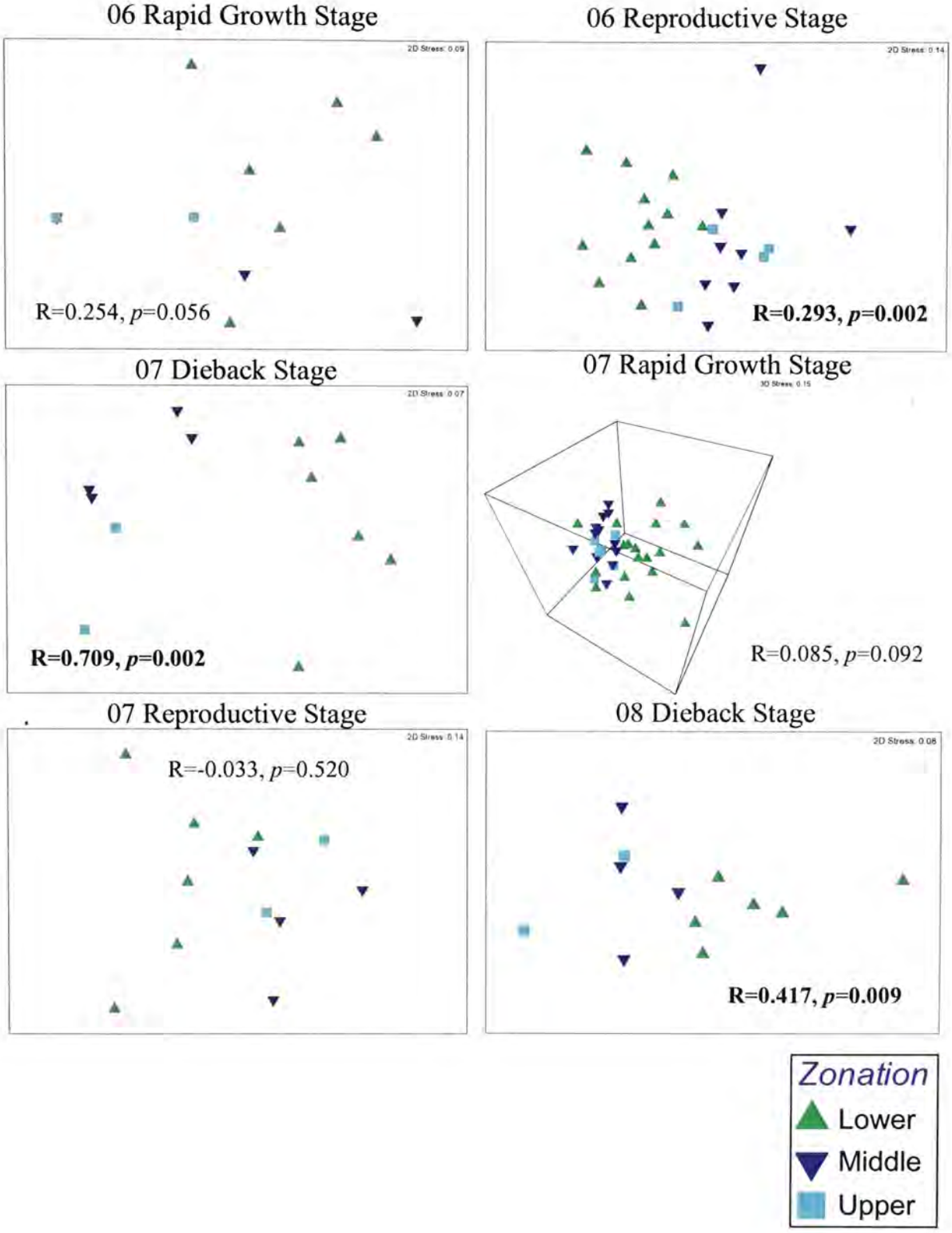


Fig. 5.21 MDS ordination plot based on Bray-Curtis similarities showing the epiphytic faunal composition along zonations of *Sargassum siliquastrum* thalli in each growth stage at LLT. ANOSIM results show significant differences in the structure of epiphytic faunal assemblages between groups during 06 Reproductive, 07 Dieback and 08 Dieback stages (marked in bold).

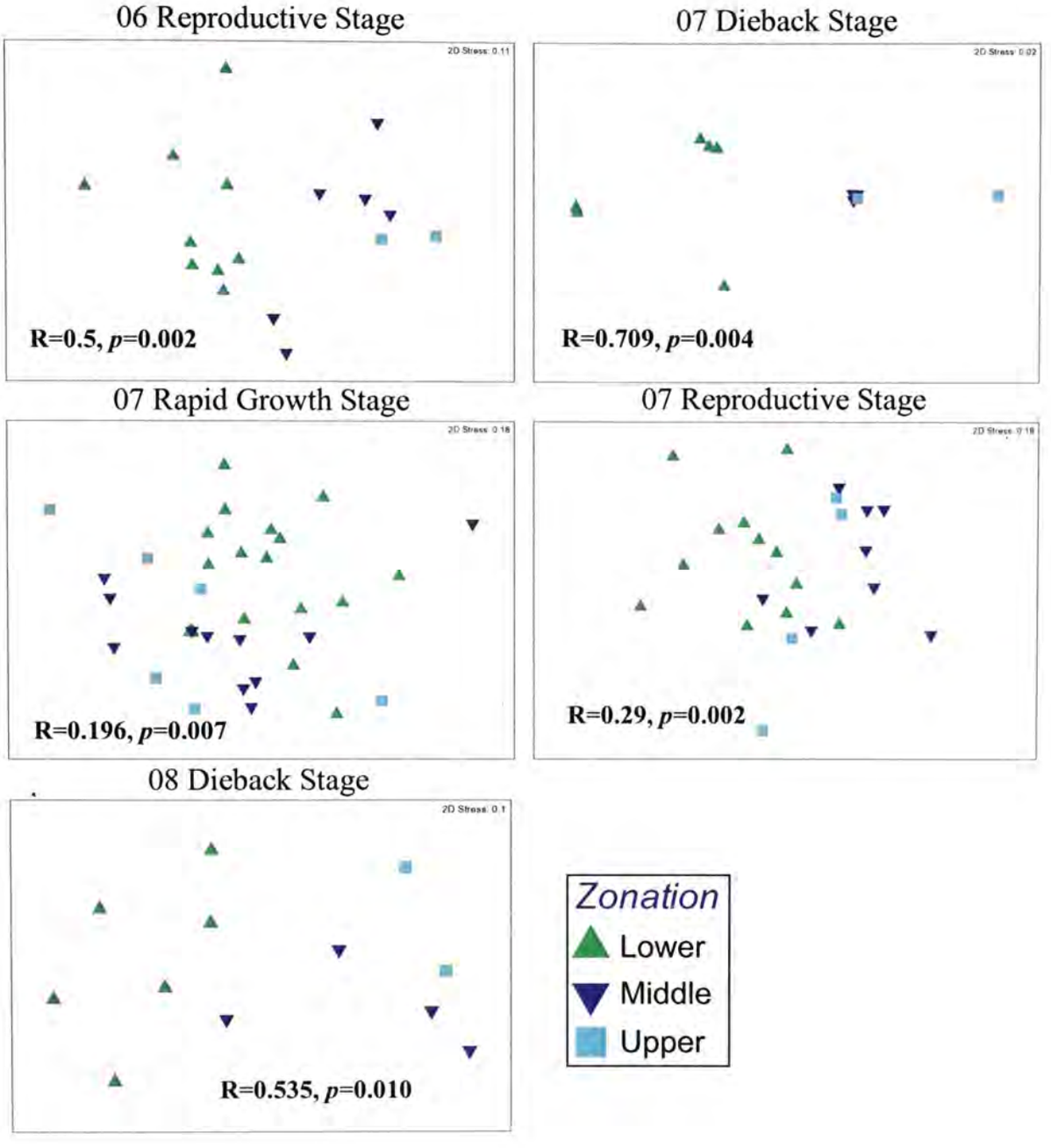


Fig. 5.22 MDS ordination plot based on Bray-Curtis similarities showing the epiphytic faunal composition along zonations of *Sargassum siliquastrum* thalli in each growth stage at LFN. ANOSIM results exhibit significant differences in the structure of epiphytic faunal assemblages between groups during all seaweed growth stages.

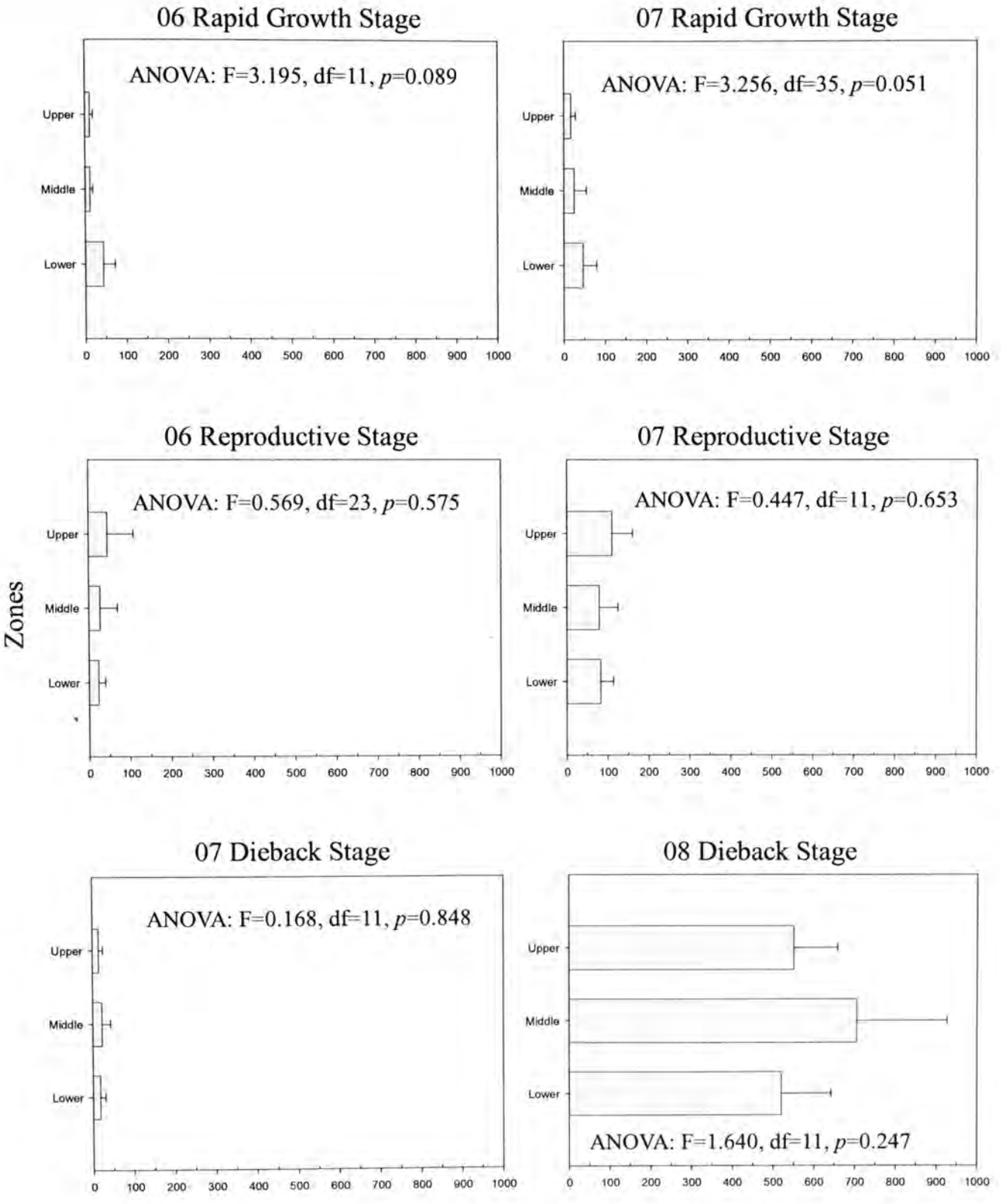


Fig. 5.23 Mean (± S.D.) epiphytic faunal density (per 100g seaweed) in each zone of *Sargassum siliquastrum* thalli in each growth stage at LLT. One-way ANOVA test results indicate no significant differences in mean faunal density among zones in all seaweed growth stages.

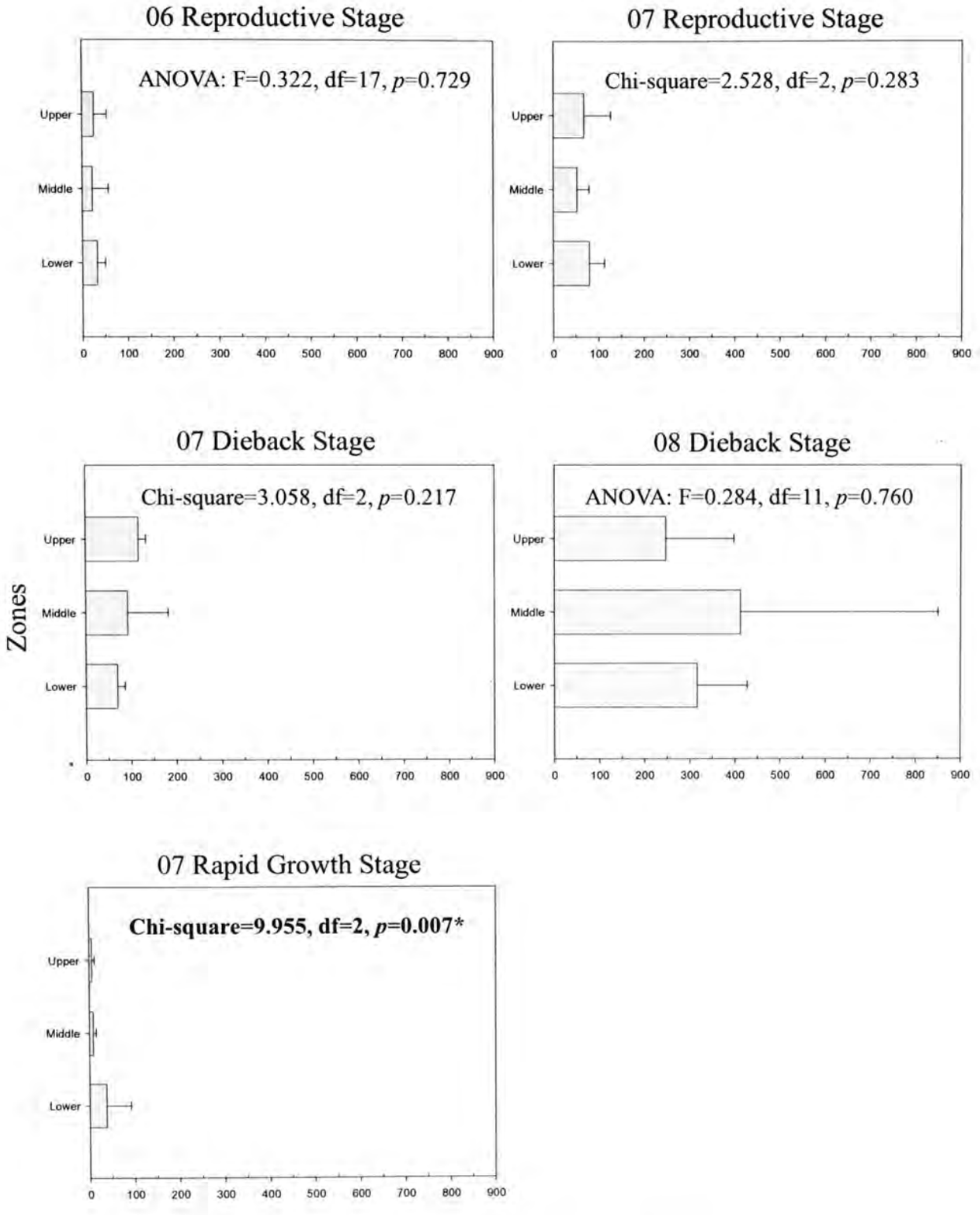


Fig. 5.24 Mean (± S.D.) epiphytic faunal density (per 100g seaweed) in each zone of *Sargassum siliquastrum* thalli in each growth stage at LFN. One-way ANOVA or Kruskal Wallis test results display significant difference in mean faunal density among zones in 07 Rapid Growth Stage only (marked in bold with *).

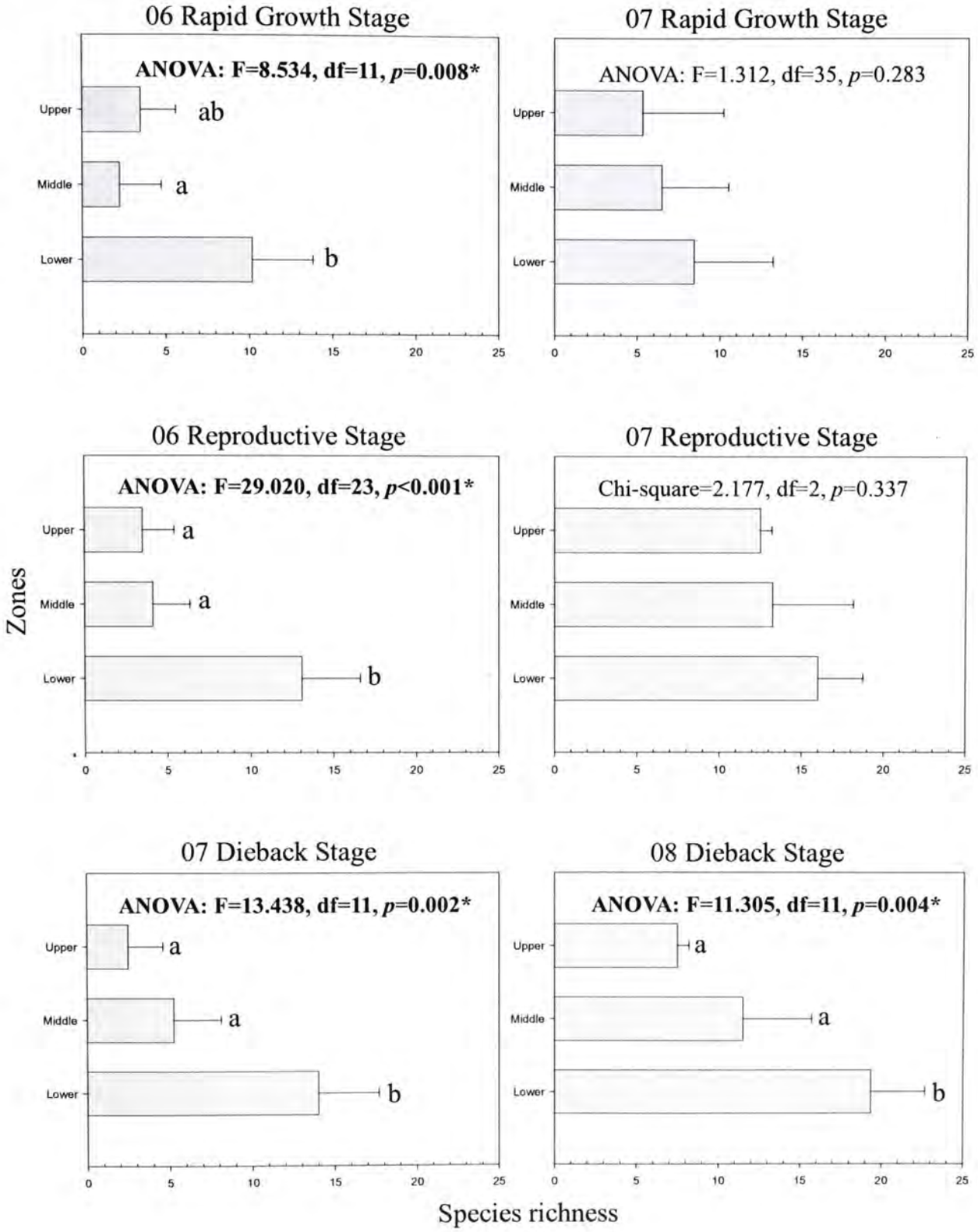


Fig. 5.25 Mean (± S.D.) epiphytic faunal species richness in each zone of *Sargassum siliquastrum* thalli in each growth stage at LLT. One-way ANOVA or Kruskal Wallis test results indicate significant differences in mean species richness among zones in all seaweed growth stages (marked in bold with *) except in 07 Rapid Growth and 07 Reproductive stages. Tukey post-hoc test identified the significant groupings among the different zones (as indicated by the same alphabets) in these growth stages.

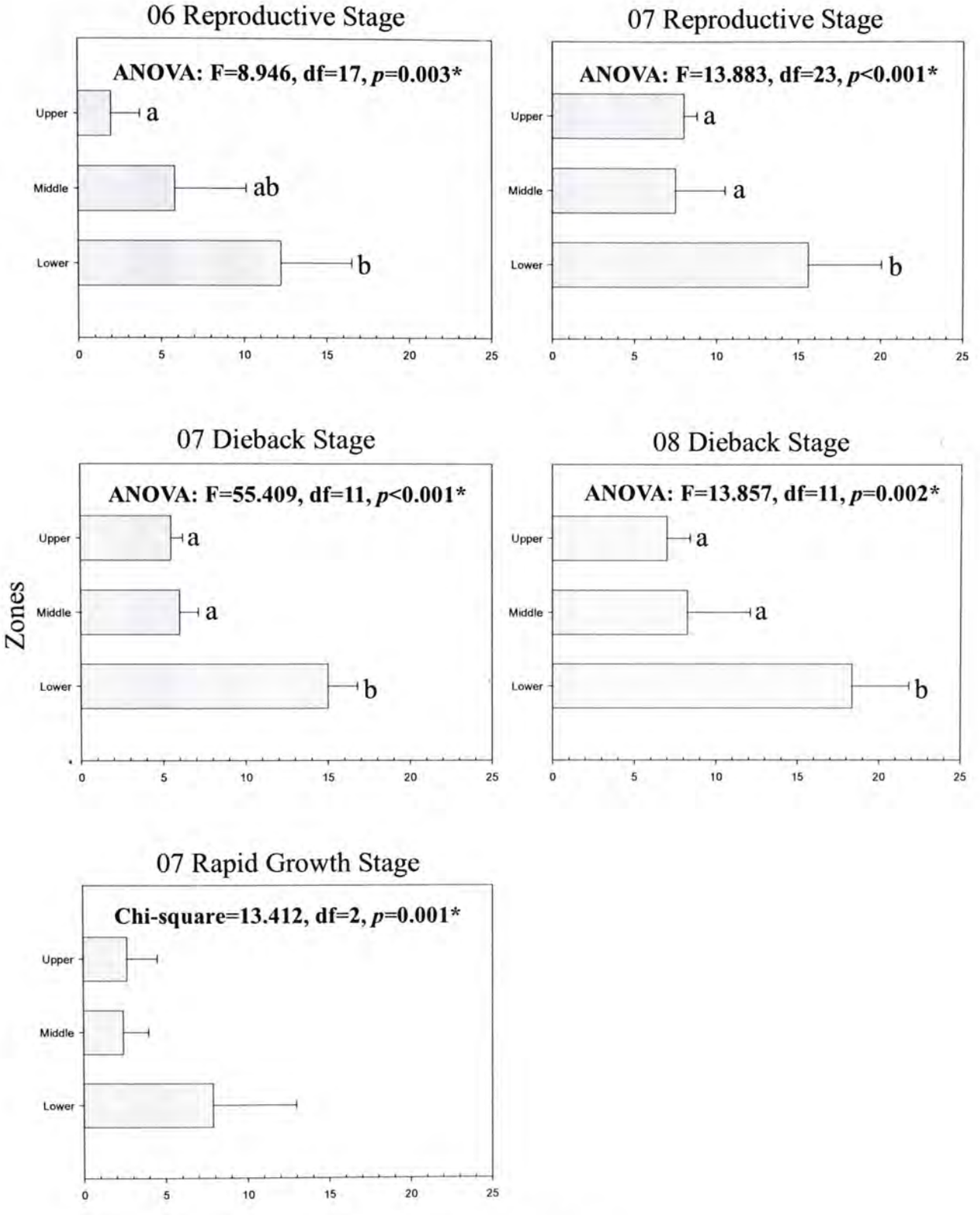


Fig. 5.26 Mean (± S.D.) epiphytic faunal species richness in each zone of *Sargassum siliquastrum* in each growth stage at LFN. One-way ANOVA or Kruskal Wallis test results indicate significant differences in mean species richness among zones in all seaweed growth stages. Tukey post-hoc test identified the significant groupings among the different zones (as indicated by the same alphabets) in these growth stages.

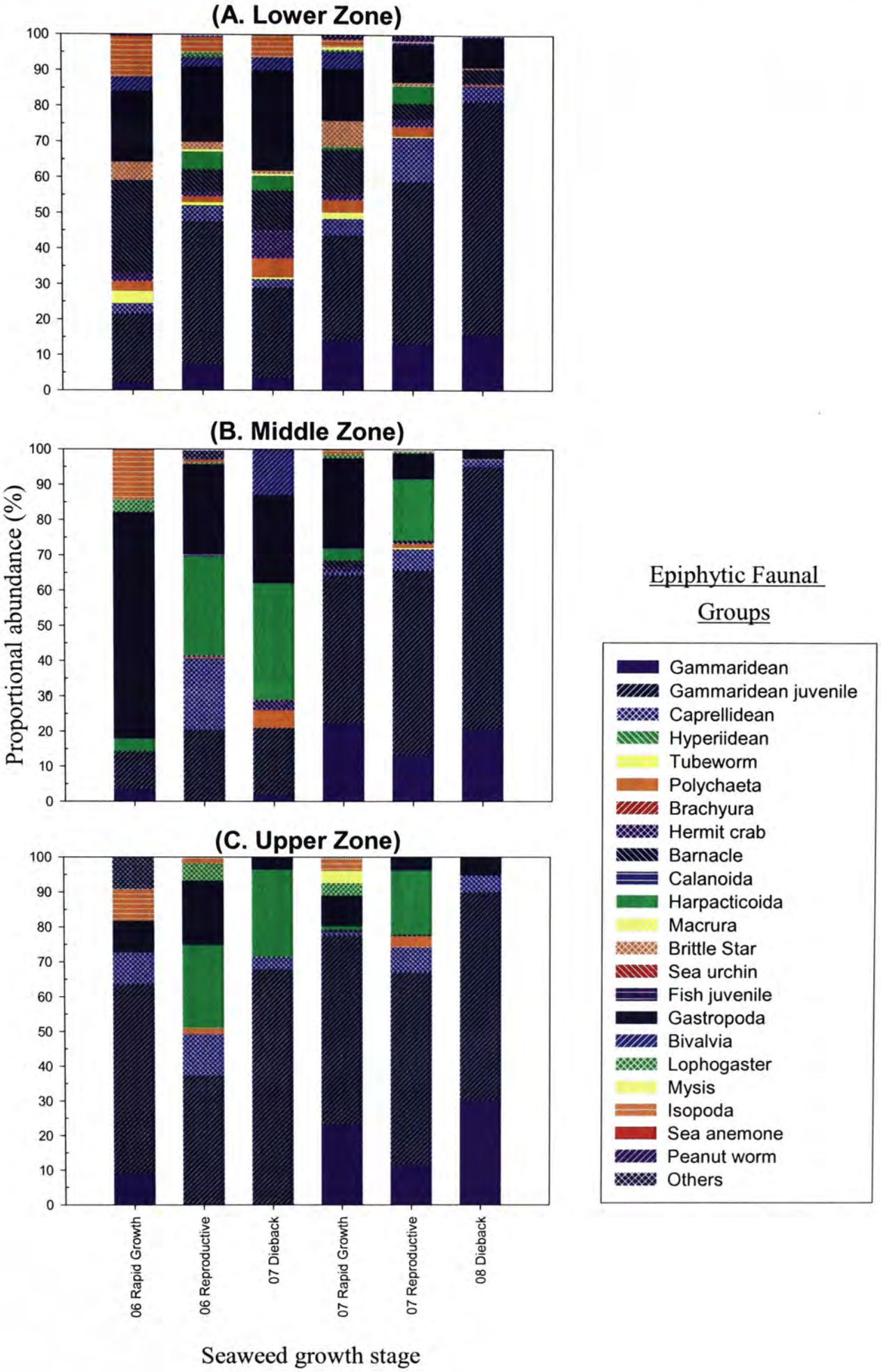


Fig. 5.27 Proportional abundance of epiphytic faunal groups in (**A**). lower, (**B**). middle and (**C**). upper zones in each growth stage of *Sargassum siliquastrum* at LLT.

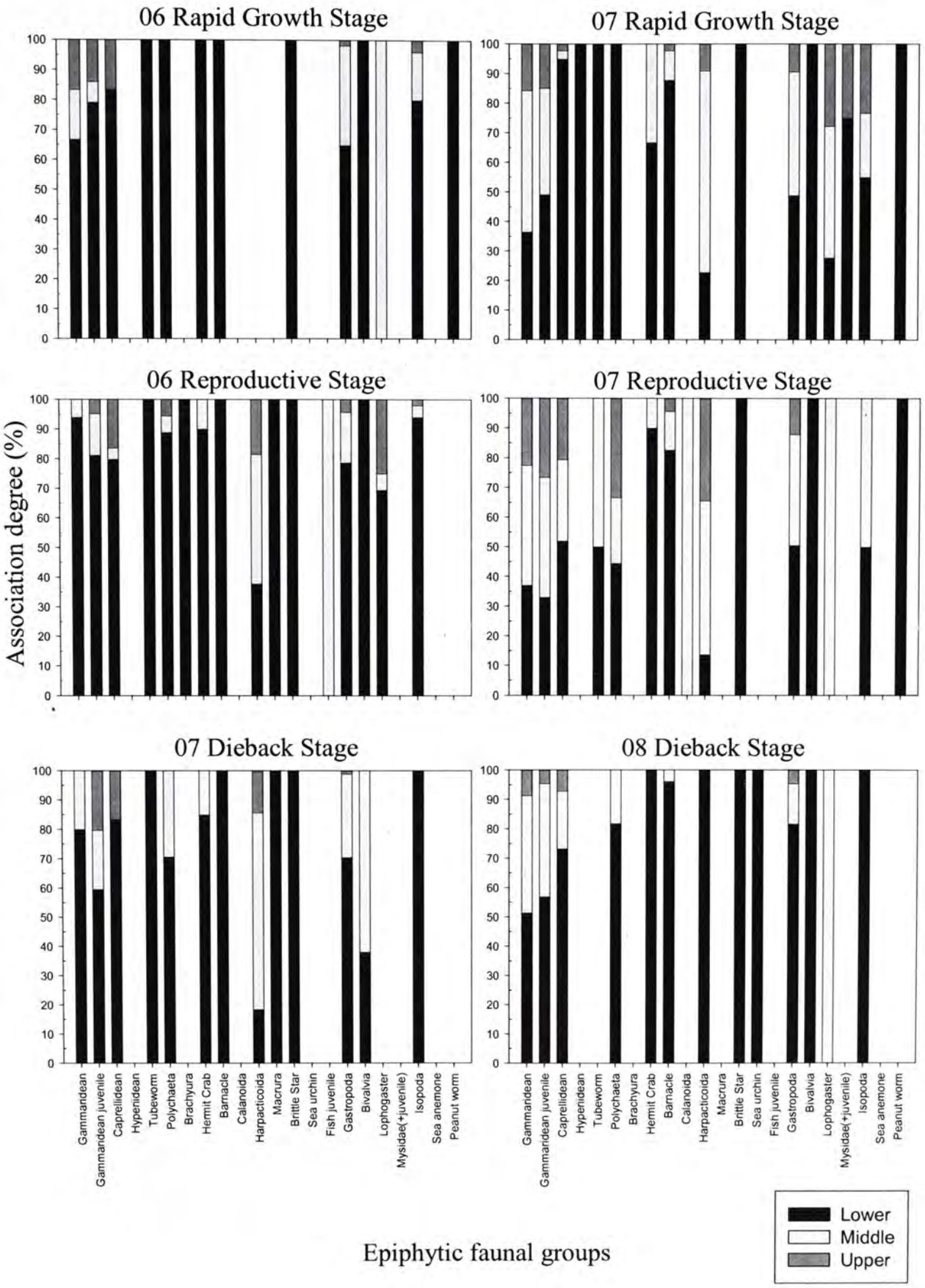


Fig. 5.28 Association degree (%) of common epiphytic faunal groups with different zones in each growth stage of *Sargassum siliquastrum* at LLT.

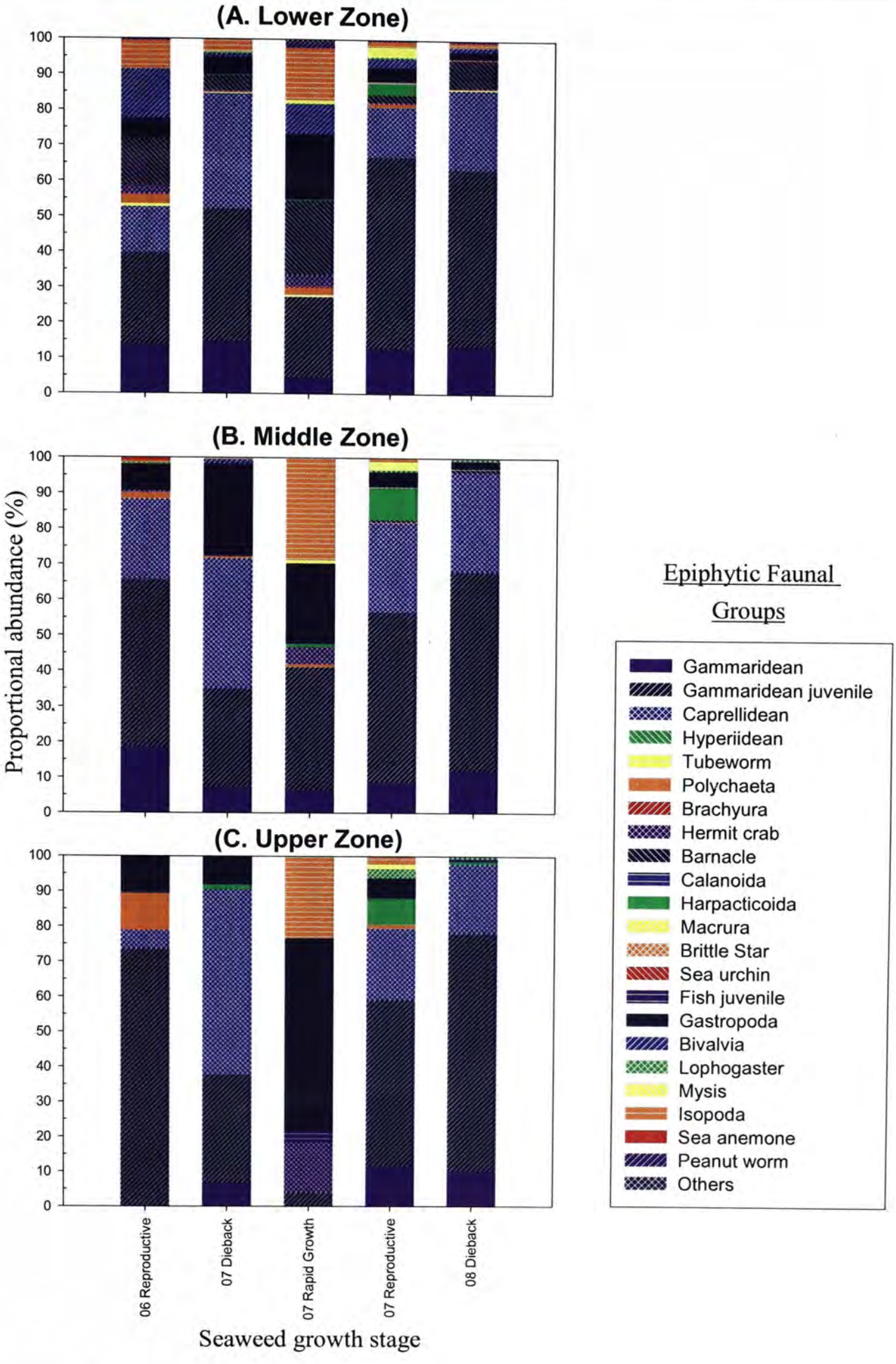


Fig. 5.29 Proportional abundance of epiphytic faunal groups in (**A**). lower, (**B**). middle and (**C**).upper zones in each growth stage of *Sargassum siliquastrum* at LFN.

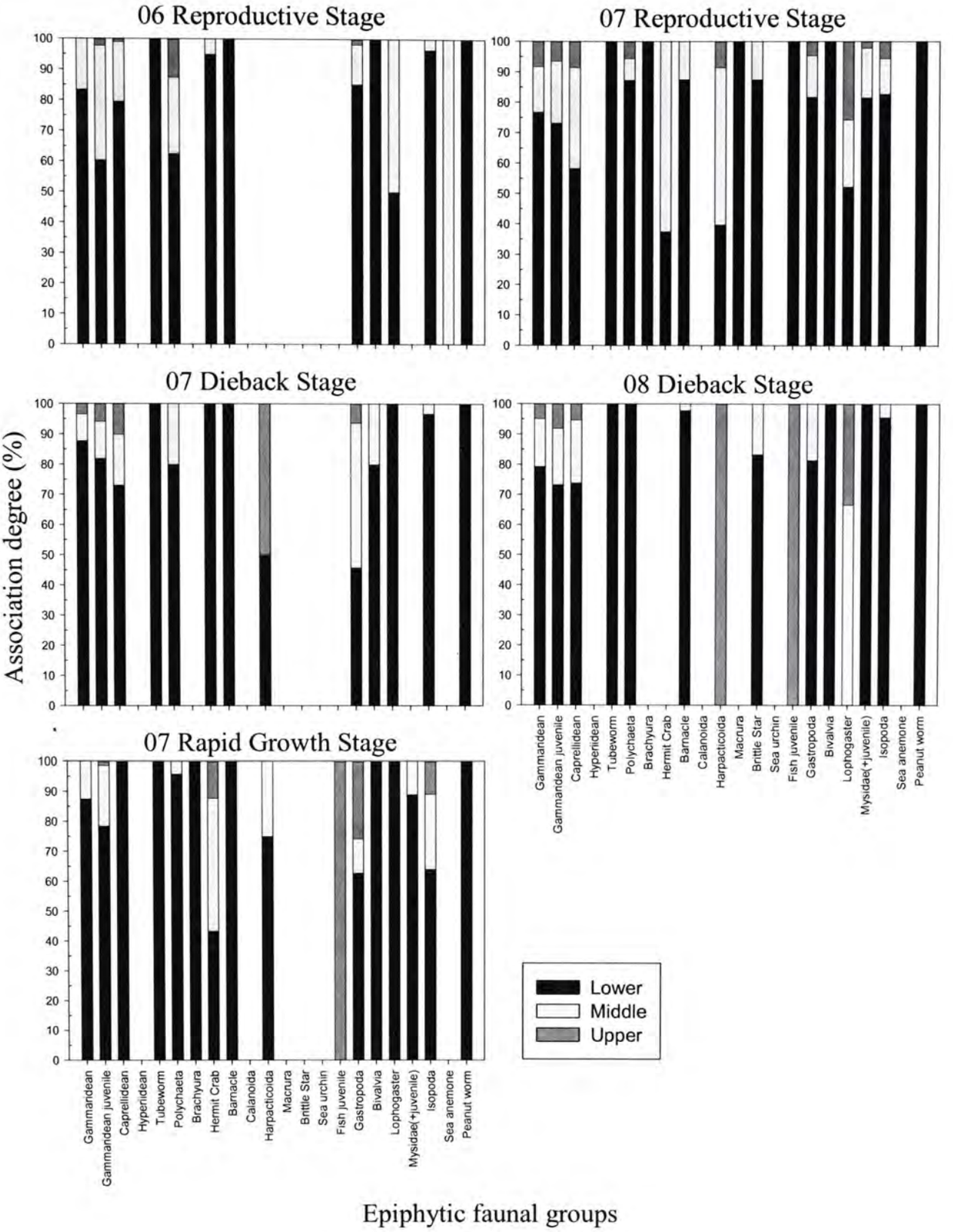


Fig. 5.30 Association degree of common epiphytic faunal groups with different zones in each growth stage of *Sargassum siliquastrum* at LFN.

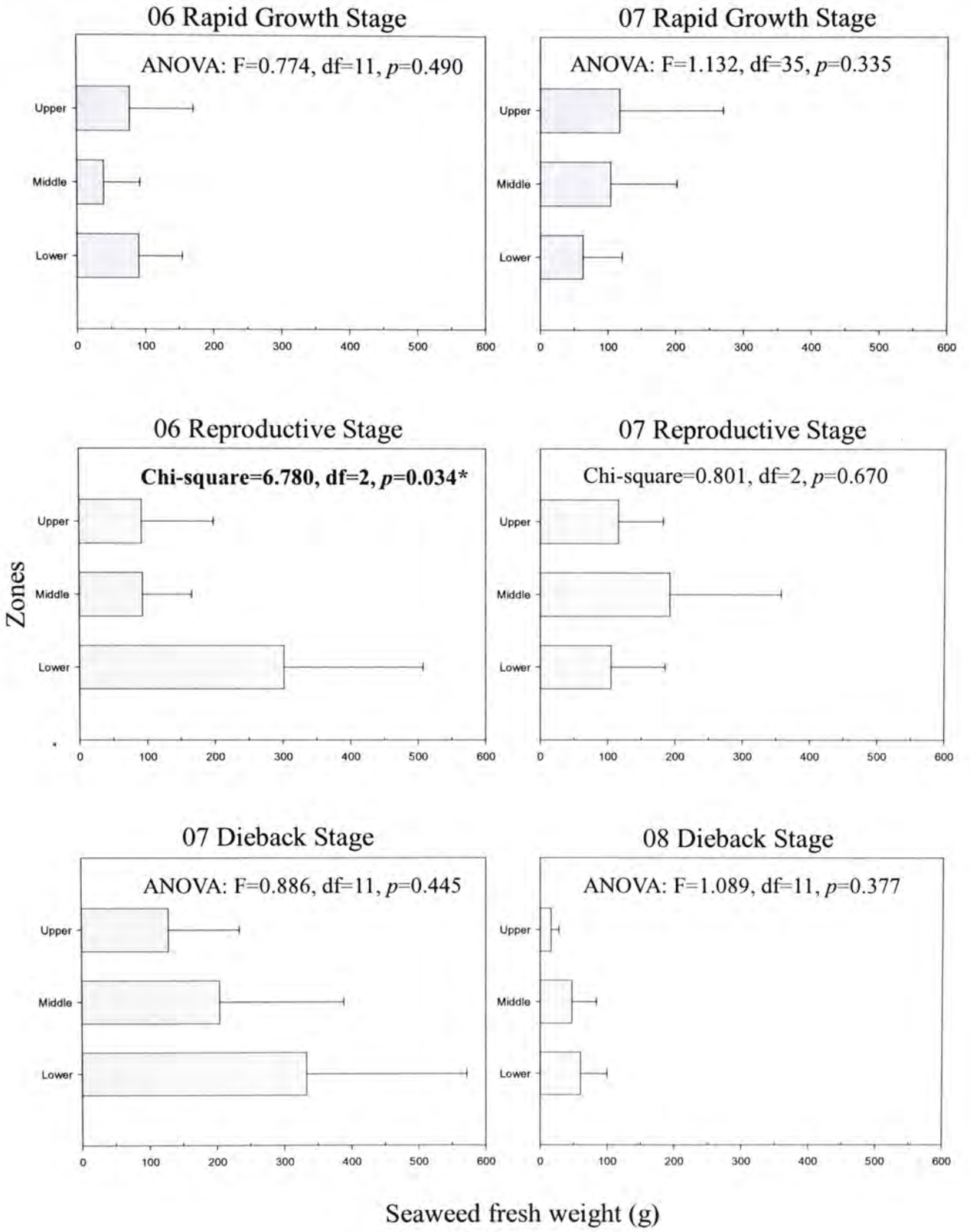


Fig. 5.31 Mean (± S.D.) fresh weight of each zone of *Sargassum siliquastrum* thalli in each growth stage at LLT. One-way ANOVA or Kruskal Wallis test results show significant difference in seaweed fresh weight among zones in 06 Reproductive stage only (marked in bold with *).

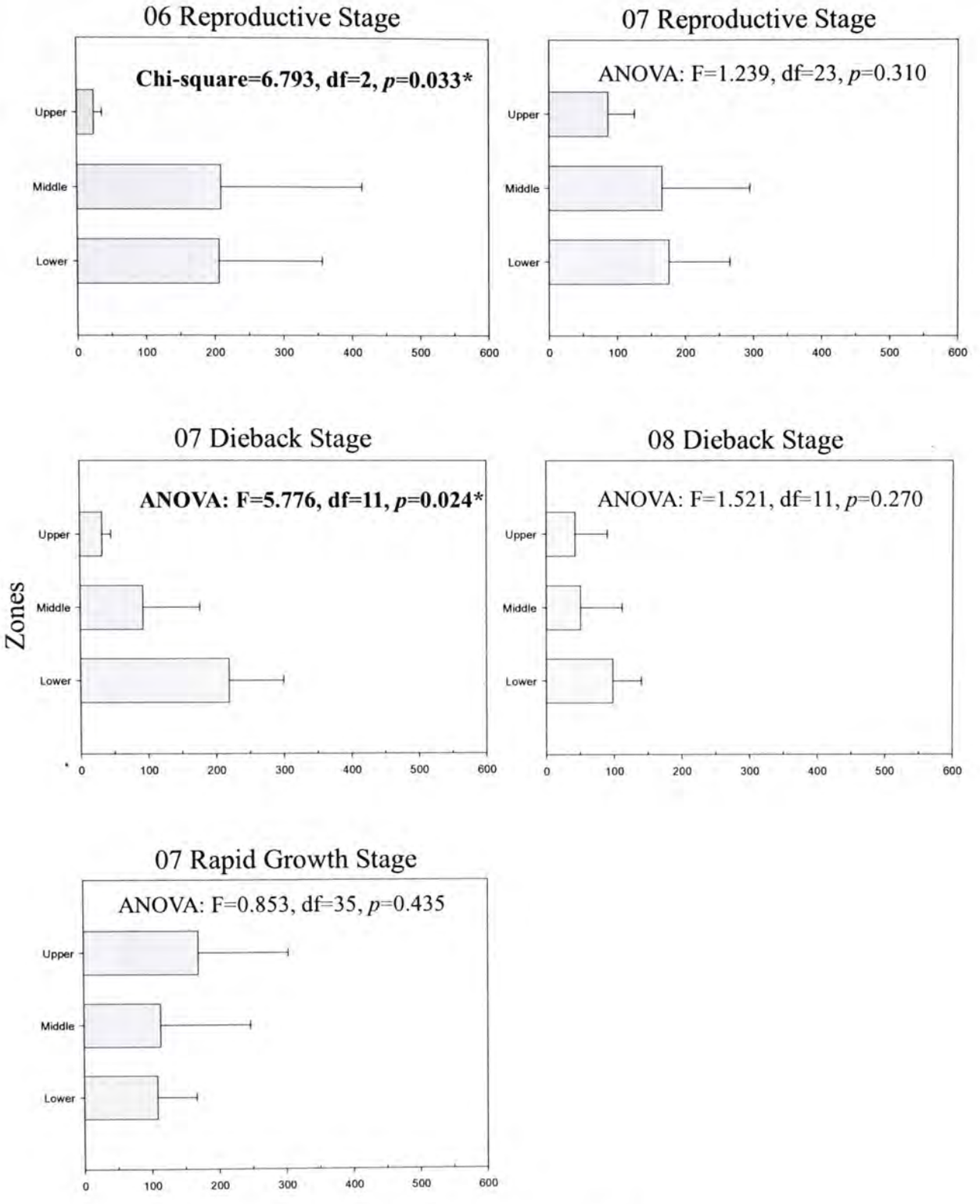


Fig. 5.32 Mean (± S.D.) fresh weight of each zone of *Sargassum siliquastrum* thalli in each growth stage at LFN. One-way ANOVA or Kruskal Wallis test results exhibit significant differences in seaweed fresh weight among zones in 06 Reproductive and 07 Dieback stages (marked in bold with *).

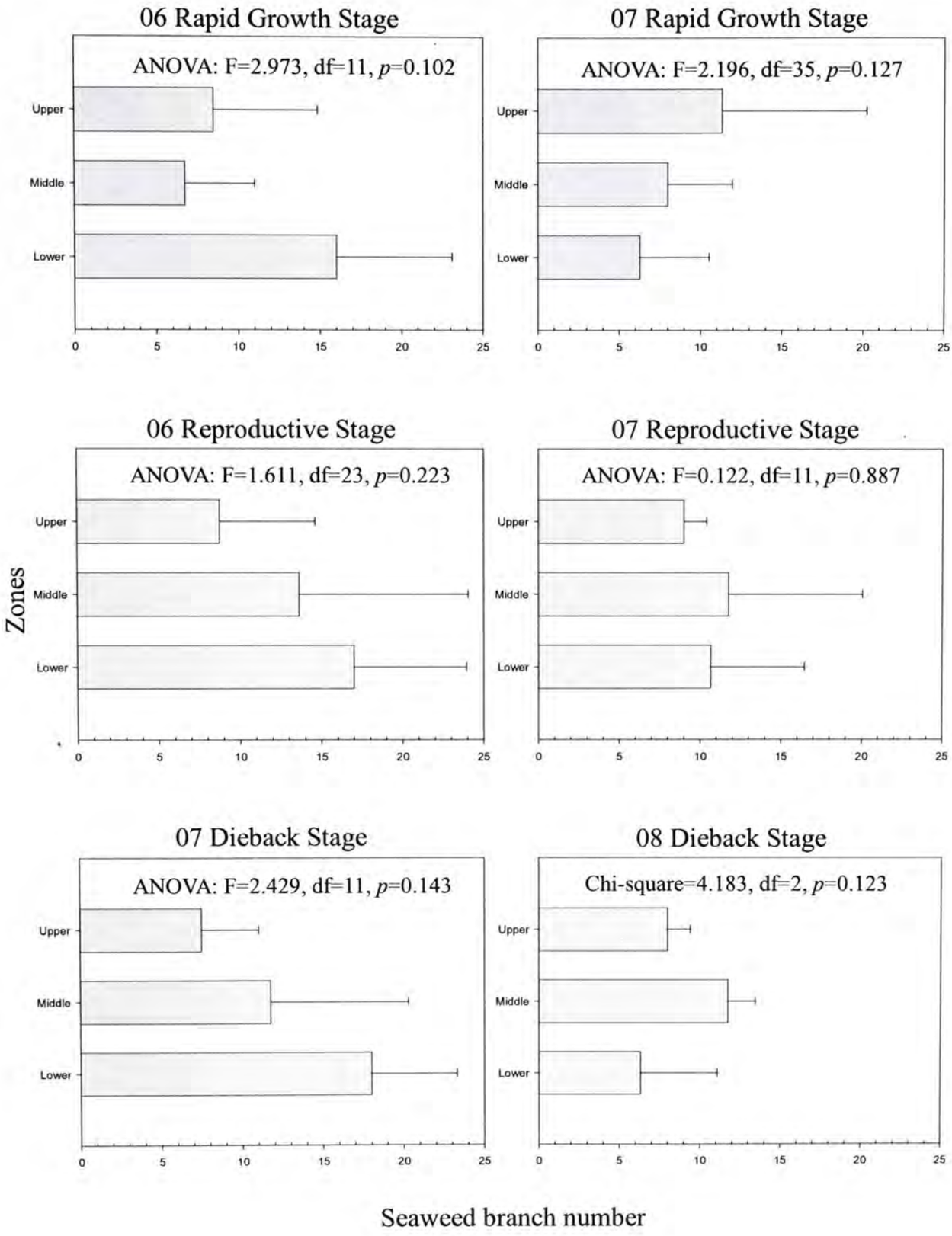


Fig. 5.33 Mean (± S.D.) branch number of each zone of *Sargassum siliquastrum* thalli in each growth stage at LLT. One-way ANOVA or Kruskal Wallis test results indicate no significant differences in seaweed branch number among zones during all seaweed growth stages.

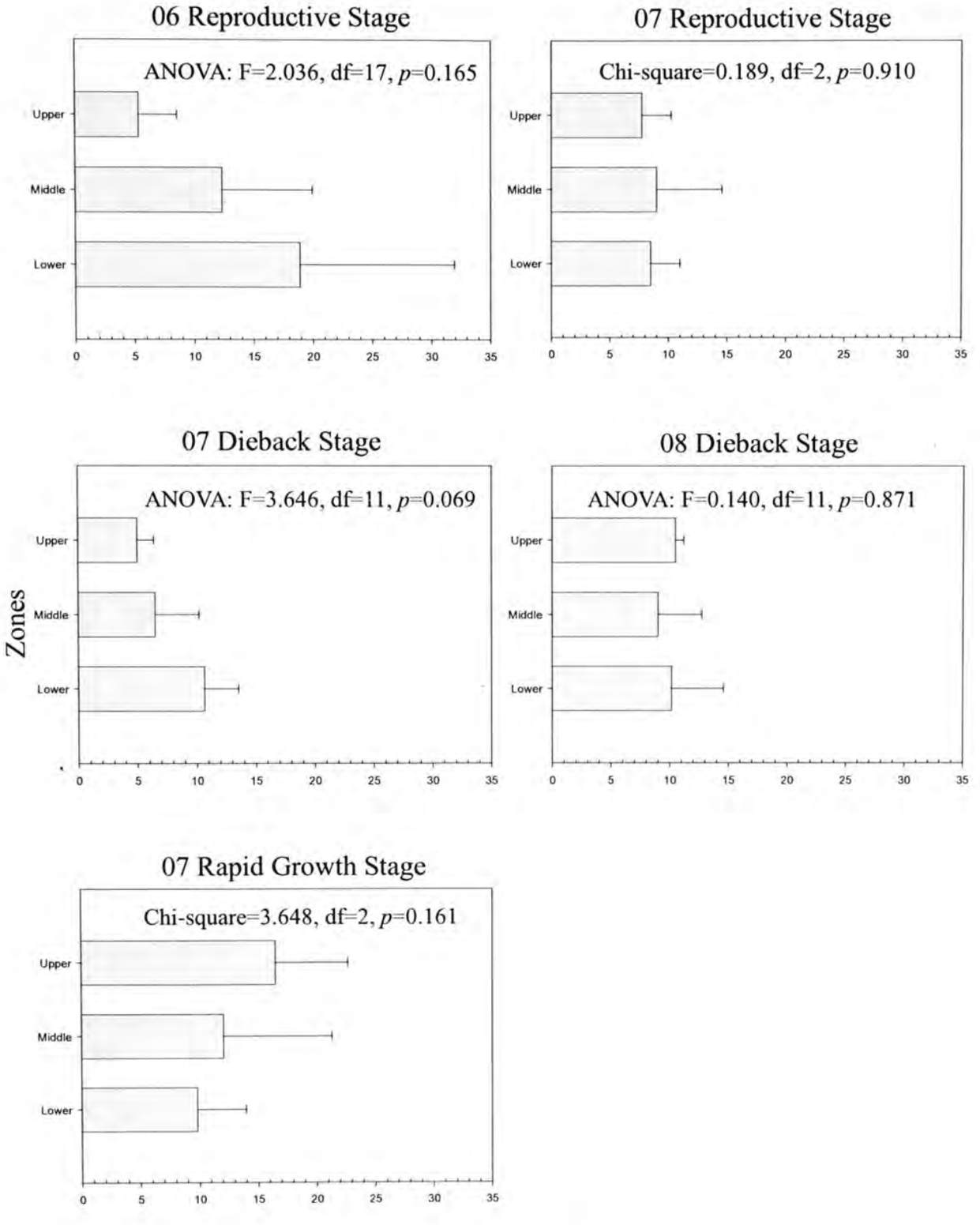


Fig. 5.34 Mean (± S.D.) branch number of each zone of *Sargassum siliquastrum* thalli in each growth stage at LFN. One-way ANOVA and Kruskal Wallis test results show no significant differences in seaweed branch number among zones during all seaweed growth stages.

Appendix: Relationship between seaweed parameters and Shannon diversity index H'

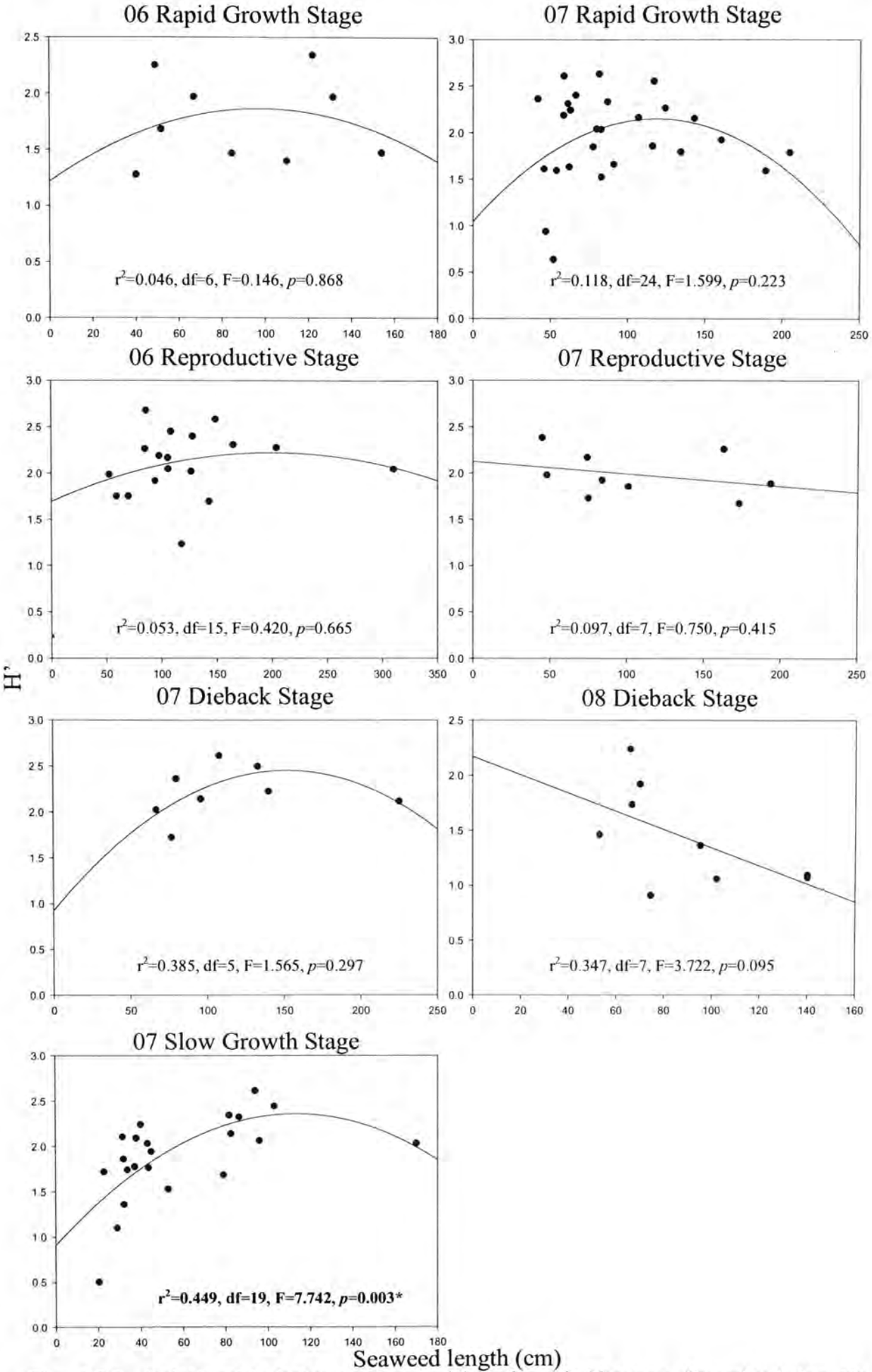


Fig. A5.1 Relationship between seaweed length with Shannon diversity index H' in each growth stage at LLT. Regression analyses indicate all relationships to be not statistically significant. Regression equations not shown.

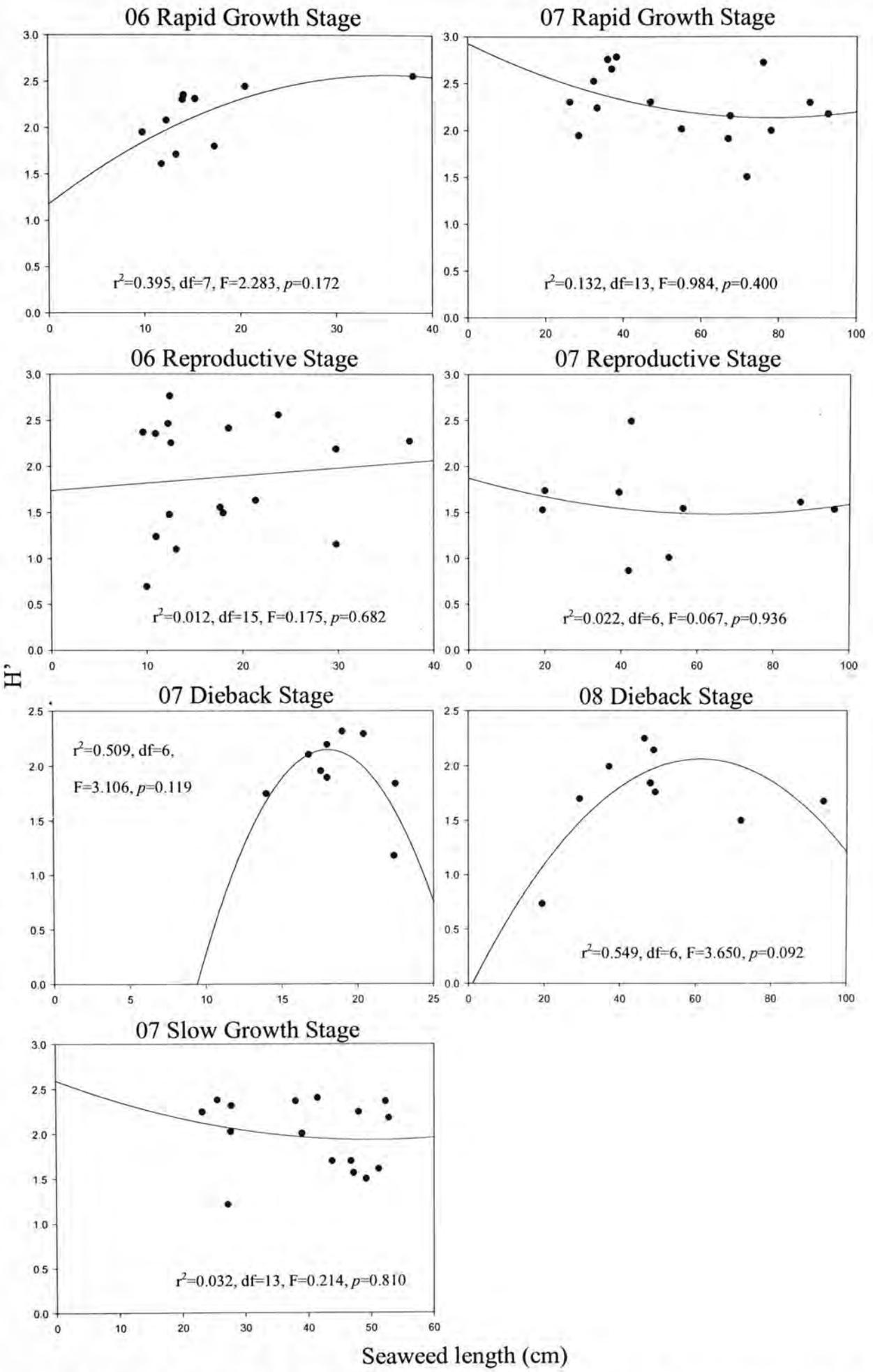


Fig. A5.2 Relationship between seaweed length and Shannon diversity index H' in each growth stage at LLS. Regression analyses indicate all relationships to be not statistically significant. Regression equations not shown.

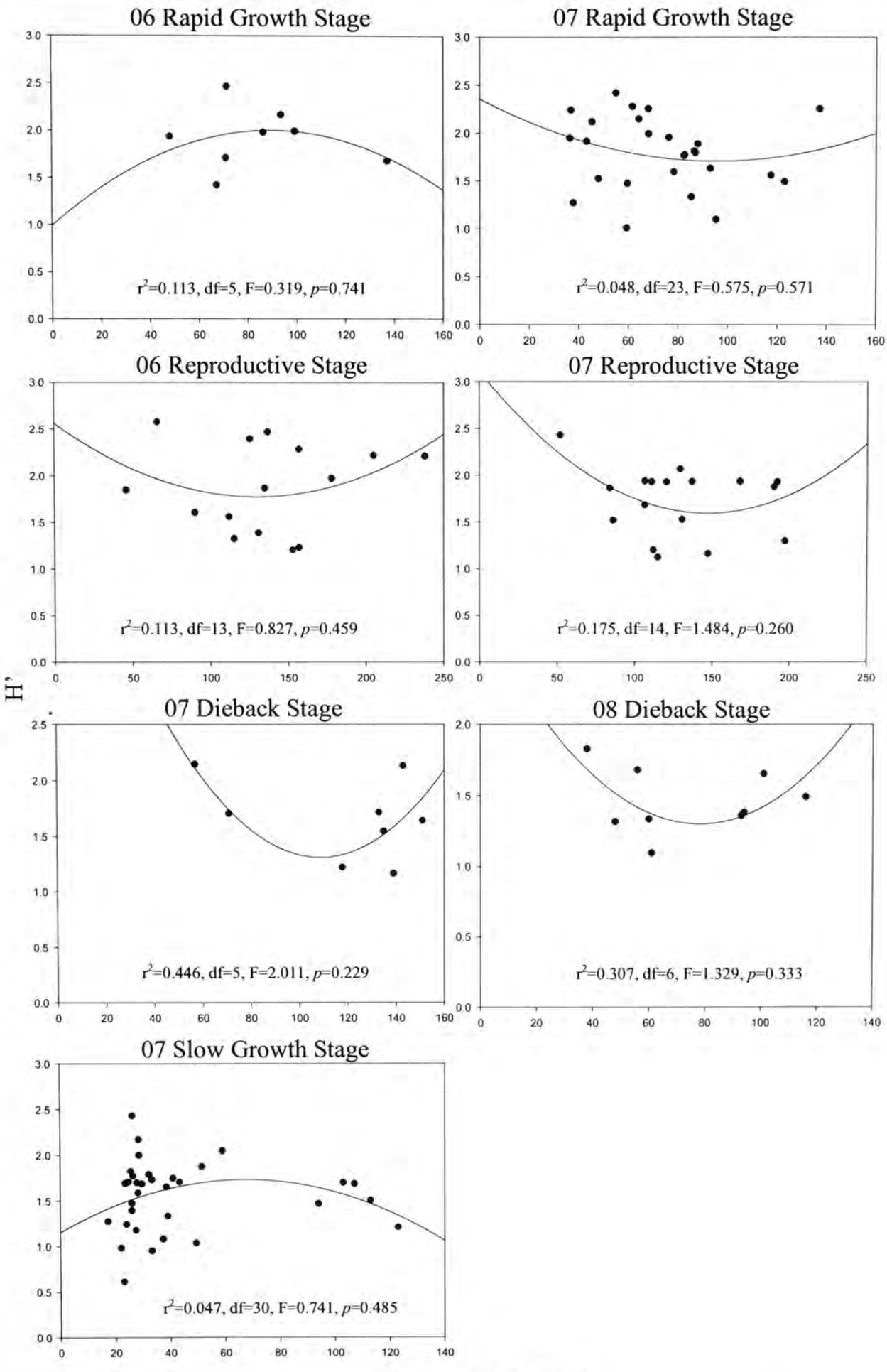


Fig. A5.3 Relationship between seaweed length and Shannon diversity index H' in each growth stage at LFN. Regression analyses indicate all relationships to be not statistically significant. Regression equations not shown.

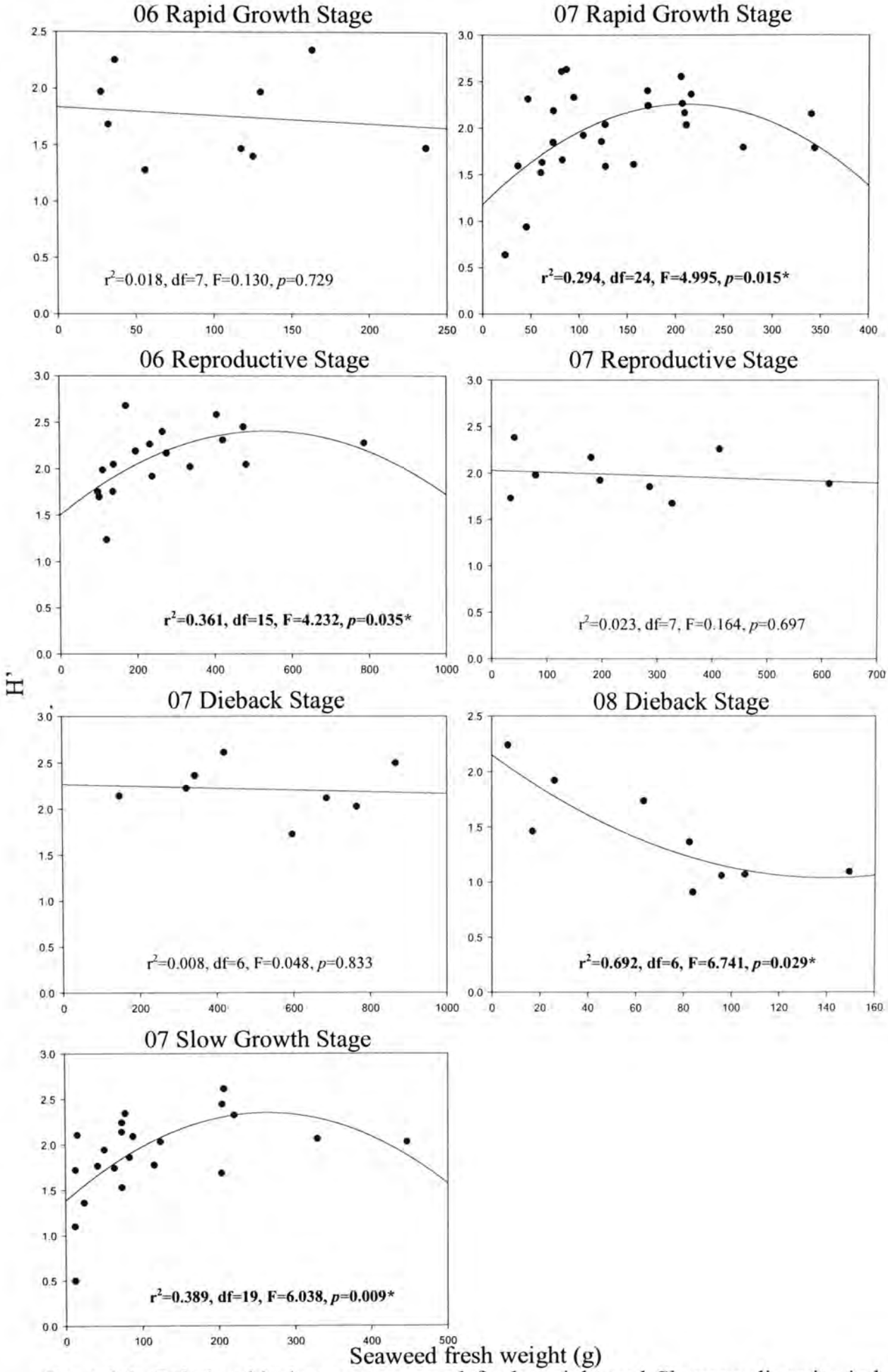


Fig. A5.4 Relationship between seaweed fresh weight and Shannon diversity index H' in each growth stage at LLT. Regression analyses indicate relationships in all seaweed growth stages except 06Rapid Growth, 07Reproductive and 07Dieback stages to be statistically significant (marked in bold with *). Regression equations not shown.

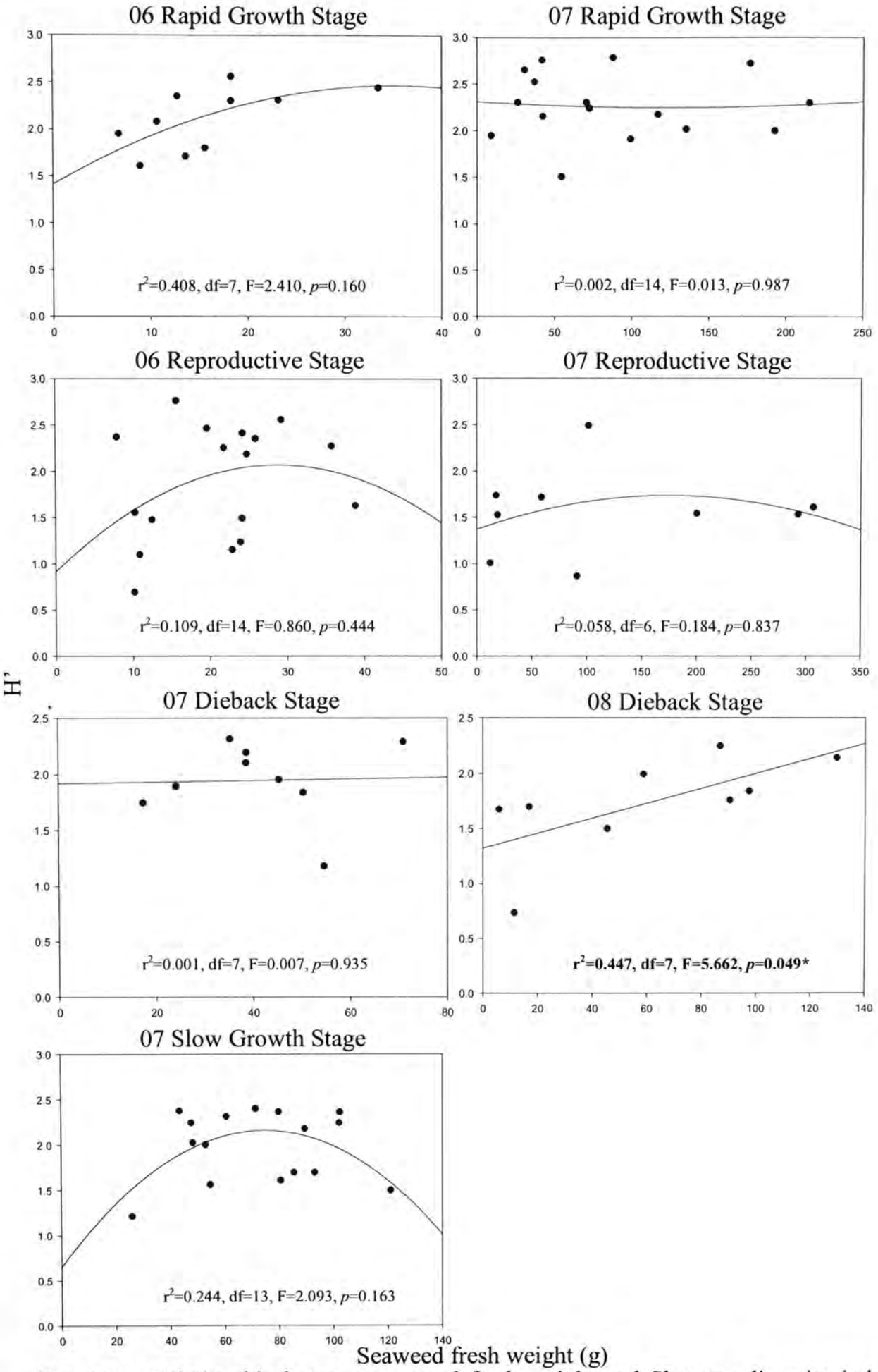


Fig. A5.5 Relationship between seaweed fresh weight and Shannon diversity index H' in each growth stage at LLS. Regression analyses indicate relationship in 08 Dieback stage to be statistically significant (marked in bold with *). Regression equations not shown.

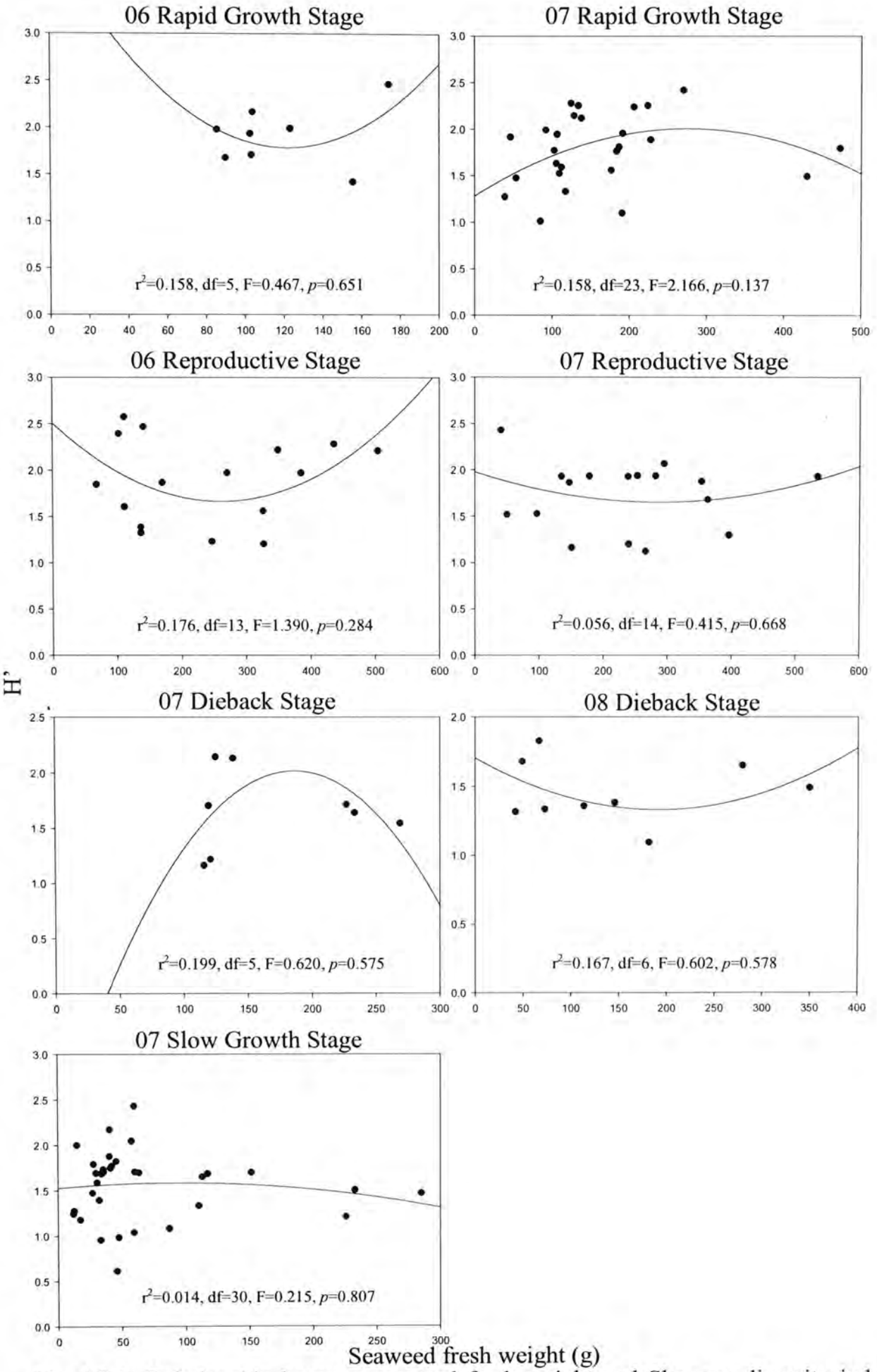


Fig. A5.6 Relationship between seaweed fresh weight and Shannon diversity index H' in each growth stage at LFN. Regression analyses indicate all relationships to be not statistically significant. Regression equations not shown.

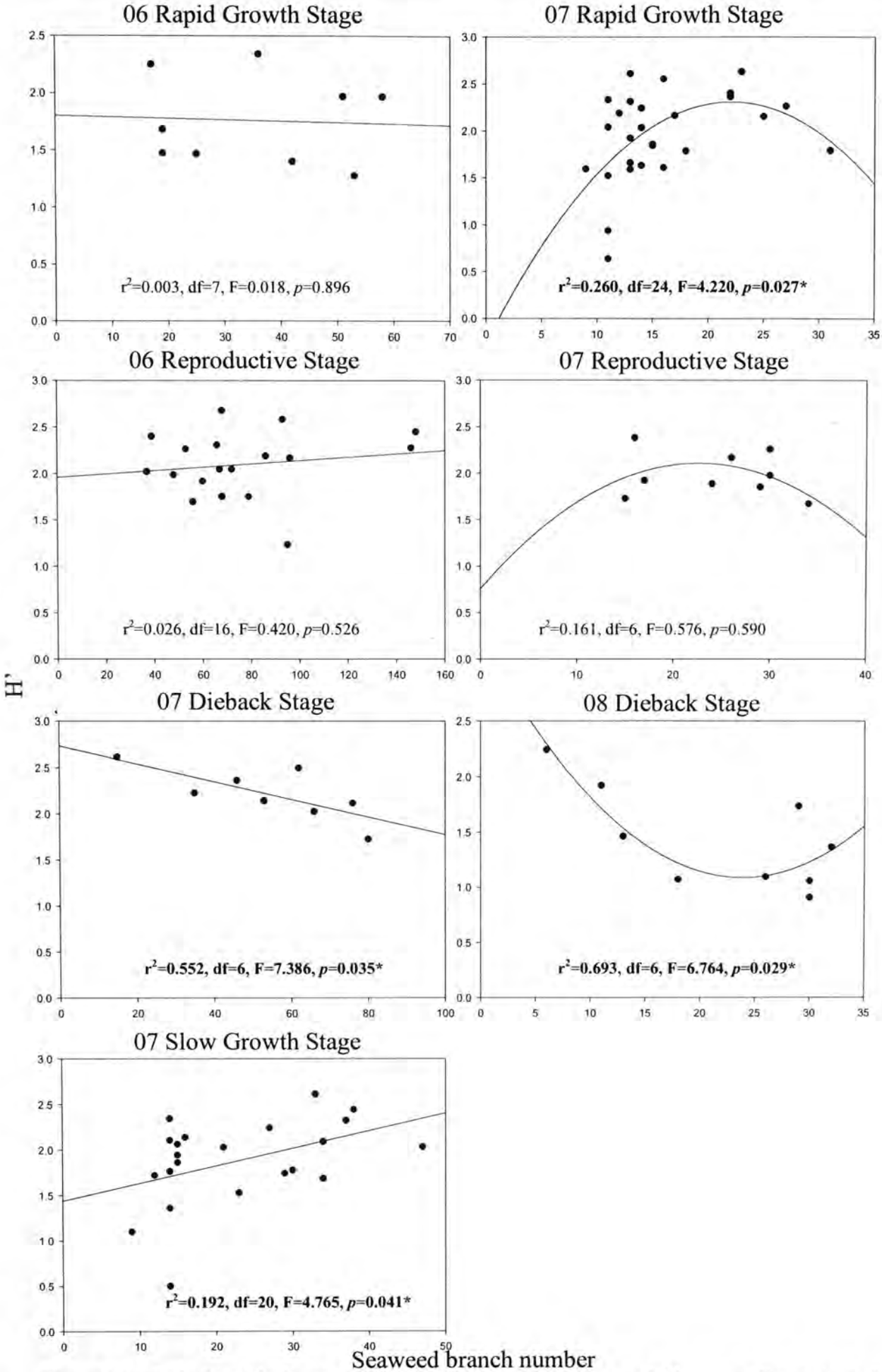


Fig. A5.7 Relationship between seaweed branch number and Shannon diversity index H' in each growth stage at LLT. Regression analyses indicate relationships in all seaweed growth stages except in 06Rapid Growth, 06Reproductive and 07Reproductive stages to be statistically significant (marked in bold with *). Regression equations not shown.

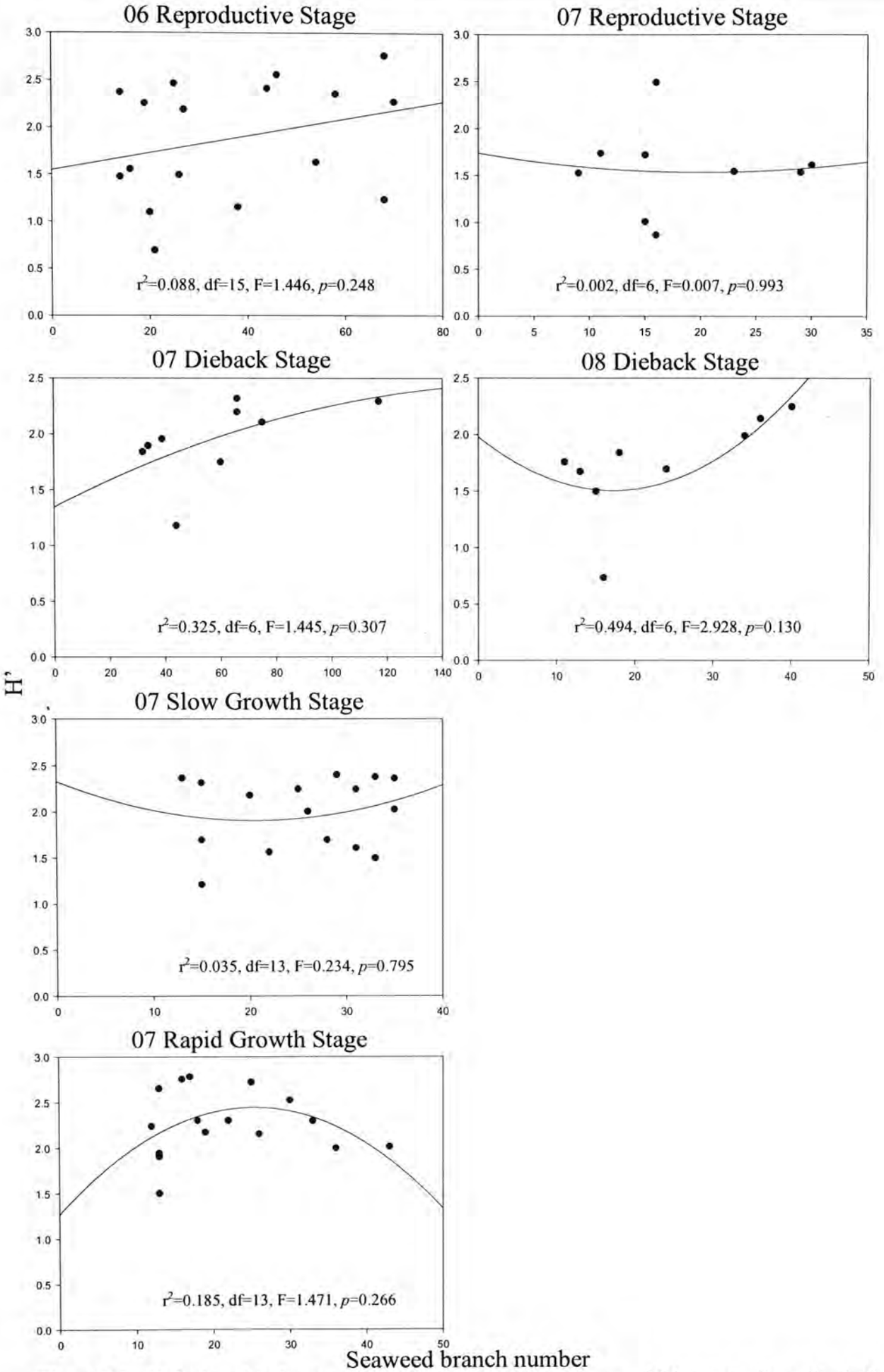


Fig. A5.8 Relationship between seaweed branch number and Shannon diversity index H' in each growth stage at LLS. Regression analyses indicate all relationships to be not statistically significant. Regression equations not shown.

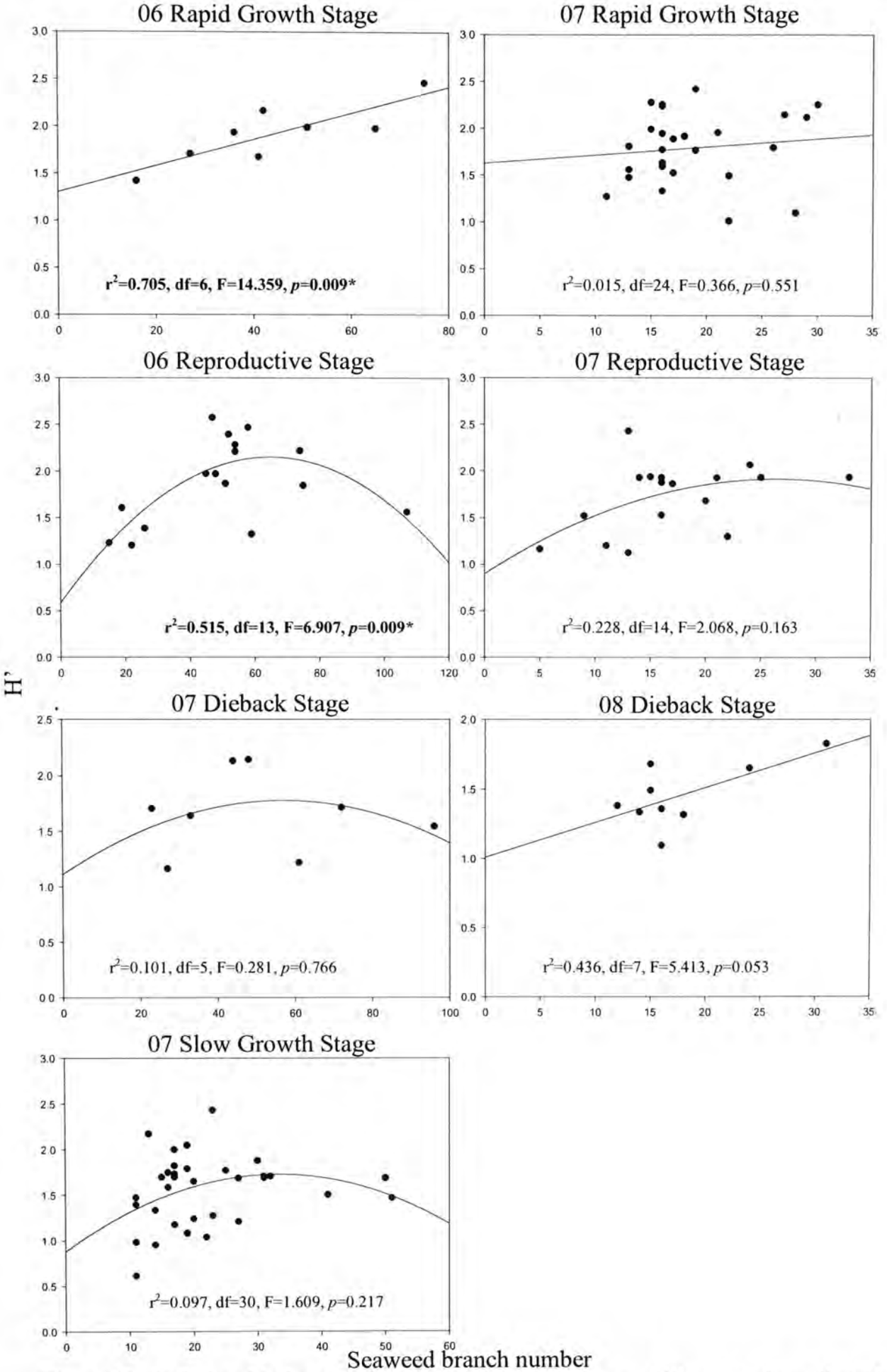


Fig. A5.9 Relationship between seaweed branch number and Shannon diversity index H' in each growth stage at LFN. Regression analyses indicate relationships in 06 Rapid Growth and 06 Reproductive stages to be statistically significant (marked in bold with *). Regression equations not shown.

Chapter 6

Synthesis and Perspectives

Seaweeds are of great economic importance. They have been extensively cultivated or harvested from the wild. Unsustainable harvesting could result in denudation of the seaweed bed and shifts in the community structure from a macroalgae-dominated to one with barren grounds, and ultimately with irrecoverable trophic cascade. Despite the general belief that seaweed bed acts as a sanctuary for ecologically and economically important marine resources, concrete evidences are difficult to come by except in a few cases involving kelp beds. The importance of seaweed ecosystem, especially those in the subtropical areas dominated by *Sargassum* spp., is often under-studied when compared with the other marine ecosystems, e.g. coral reef. The importance of subtropical areas as a refuge for tropical species is becoming more apparent given the imminence of global warming and climate change. In subtropical Indo-west Pacific where Hong Kong is located, only one study (Lee 2000) on the epiphytic faunal community structure associated with intertidal seaweed community has ever been done. No other studies in subtidal seaweed beds have been performed nor was there any evaluation of the zooplankton assemblages associated with the

seaweed beds. It is therefore essential to fill in the knowledge gap of the role of subtropical seaweed bed as a marine habitat to contribute to the general understanding of the dynamics of Hong Kong marine environment in general and its associated faunal communities in particular. Only by collecting the baseline information on seaweed community can its ecological value as a breeding and nursery ground for marine organisms be properly assessed. An appropriate strategy can then be installed in assessing environmental impacts caused by coastal developments, which are the major threats to the coastal macroalgal communities; as well as in formulating sustainable practices in seaweed harvesting that could be applied globally in other places such as in China and in other Southeast Asian countries. Hence, in this study, the faunal assemblages, including the epiphytic fauna and zooplankton in the extensive bed of the brown seaweed *Sargassum siliquastrum* in Hong Kong eastern waters were examined to assess their temporal variation from November 2006 to January 2008. In addition, the relationships between faunal structure and the *Sargassum siliquastrum* phenology (i.e. slow growth stage from March to August; rapid growth stage from September to November; reproductive stage from December to January; and die-back stage from January to February), the seaweed structural complexities, as well as the environmental parameters in the seaweed bed were explored.

Throughout the sampling period, a total of 72 species and/or taxonomic groups of zooplankton were recorded in both sites in the Hong Kong eastern waters: Lung Lun Tsui (LLT) in Tung Ping Chau Marine Park (TPCMP) and Lo Fu Ngam (LFN) in Sai Kung. Zooplankton abundance and species richness were relatively higher from January to March, September and November 2007 in both sites. Seasonal variations in abundance and species composition were likely brought about by the prevailing monsoons and discharge from the Pearl River. Zooplankton assemblage structure in the *Sargassum siliquastrum* bed was more distinctly different from that in the unvegetated habitat especially during rapid growth, reproductive and dieback stages of *Sargassum siliquastrum*. Difference in species richness contributed to this distinct difference in the zooplankton assemblage structure. This was more significantly influenced by the seaweed phenology, as indicated by changes in the seaweed length over time, than by the variations in physical environmental factors. The close association between zooplankton assemblage structure and seaweed phenology was likely due primarily to the substantial supply of food sources by the seaweed thallus itself and the phyto-detritus generated, especially during times of reproduction and dieback of *Sargassum siliqaustrum*. The complex structure offered by the vegetation, in particular the dense canopy during the rapid growth, reproductive and dieback stages of the seaweed was also important. The role of the extensive *Sargassum*

siliquastrum beds as a nursery and nesting ground for zooplankton was highlighted.

Being of high productivity, the *Sargassum siliquastrum* canopy provides its associated zooplankton with ample supply of food and a refuge with hydrodynamically more stable environment. In this study, the removal of seaweed canopy resulted in an impact on the zooplankton assemblage structure. This was evidenced by the change in canopy removed treatment samples showing a progressive similarity with unvegetated samples while becoming distinctly different from the controls where seaweed canopies remained intact. Effect of canopy removal on zooplankton species richness was more serious than on its abundance. This is consistent with the findings that difference in species richness was the main reason causing significant difference in the zooplankton assemblage structure between vegetated and unvegetated habitats. Removal of seaweed canopy led to a loss of certain associated species and their juveniles, such as mysids, lophogasters, fish and squids. This provided additional evidence to indicate the role of *Sargassum siliquastrum* canopy as a site for larval retention and as larval nursery ground.

Apart from the zooplankton assemblage, the epiphytic faunal community associated with the seaweed bed of *Sargassum siliquastrum* and its temporal variation was also

investigated in this study. Through the whole course of sampling, a total of 163 species (including morpho-species) and taxonomic groups of epiphytic organisms on *Sargassum siliquastrum* were identified in three sites, LLT, LLS (Lung Lok Shui) and LFN, in Hong Kong eastern waters. Seaweed beds were shown to function as site for larval settlement and recruitment of epiphytic faunal species, particularly during the rapid growth, reproductive and dieback stages of *Sargassum siliquastrum*. Synchronization of faunal life cycles, e.g. reproductive period, with the phenology of *Sargassum siliquastrum* was illustrated. The peak in total faunal abundance and species richness in late winter and early spring (Apr07, May07 and Feb08) was due to the seasonal flux of some common groups, namely gammarideans, caprellideans, isopods, gastropods and harpacticoids, in plenteous number. This phenomenon is believed to be supported by the seasonal burst of food items, i.e. host macroalgal thallus tissue, the epiphytic algae and their phyto-detritus, of higher quality and quantity, together with the lowering of seaweed anti-herbivory and anti-fouling defense in the form of lower levels of secondary metabolites during the reproductive and dieback stages of *Sargassum siliquastrum*. In addition, *Sargassum siliquastrum* bed acted as nursery and nesting grounds for ecologically and economically important fishery species, notably mantis shrimp, lobster and common rockfish. The essence of seaweed bed as a nursery habitat was also evident even during the slow growth stage

of *Sargassum siliquastrum*. Environmental factors, namely temperature, dissolved oxygen and salinity levels, were unlikely to exert an immediate effect on the epiphytic faunal assemblage.

The connection between epiphytic faunal assemblage structure with physical properties, such as length, branch number and biomass, of *Sargassum siliquastrum* was investigated. The within-plant faunal zonation of *Sargassum siliquastrum* was also exhibited in this study. The increase in the physical properties of *Sargassum siliquastrum* generally produced concomitant increase in the abundance and diversity of the associated faunal community. The macroalgal biomass, expressed as fresh weight, exerted greater effects on epiphytic faunal abundance and species richness, particularly during seaweed reproductive and dieback stages, when compared with other components of structural complexity. The provision of affluent food source (i.e. host plant tissue, epiphytic plant and phytodetritus), enhanced surface area for attachment and protection, as well as amelioration of the strong hydrodynamics, were probably factors that led to the augmentation of faunal numbers and species diversity by an increase in seaweed biomass. In terms of structural complexity alone, seaweed branch number imposed a relatively more influential positive effect on epiphytic faunal abundance and species richness, especially during times of seaweed rapid

growth and reproduction, when compared with seaweed length. The increase in faunal abundance and species richness with increase in branch number might be attributable to an increase in habitable space between branches for the fauna to attach and to stay away from predation. Within-plant zonation pattern was more pronounced in seaweed reproductive and dieback stages. Species richness and abundance were in the main, highest in the lower zone of the algae, including the holdfast. This was possibly due to an increase in the surface area of the algae for faunal colonization and in structural complexity for better protection from physical stress and predation, as a result of greater biomass of the lower zone. In general, faunas resided in lower zone of *Sargassum siliquastrum* were more sedentary and were mostly herbivorous or detritivorous; while fauna associated with middle or upper zone were more mobile. On the whole, no one particular macroalgal physical parameter can be singled out as the determining factor in controlling the observed epiphytic faunal composition. It is preliminarily believed that food availability, and not predation pressure, was the limiting factor. This is supported by the findings in the present study, with respect to the structural complexity of both the algal plant and the within-plant zonation, that the associated epiphytic faunal assemblage was more dependent on the availability of macroalgal biomass than on any of the other parameters considered.

Variation in the structure of faunal assemblage associated with the seaweed bed was a result of intermingle of several biotic mechanisms, namely trophic interactions, reproductive biology, together with the structural complexity, phenology and chemical defense of seaweeds. Additional ecological consequences of canopy removal should be explored, especially given that canopy removal has been the strategy used in the harvesting of many canopy forming species, in order to maintain sustainable exploitation of these seaweed resources. Effects of predation pressure and intra- and inter-competition in structuring the faunal community should as well be evaluated. Although environmental factors were found to exert no immediate effect on the epiphytic faunal assemblage in this study, additional monitoring on the physical parameters, such as nutrient loads and solar irradiances, of the water environment should still be carried out to further investigate the effects of external abiotic environment on epiphytic faunal assemblage structure in the *Sargassum siliquastrum* bed. Effects of the environmental factors may be long term and may not be readily detected in a short term experiment like that carried out in the present study.

Overall, this study provides a foundation for highlighting the conservation values of seaweed beds as a potential nursery and nesting ground for numerous zooplankton as well as epiphytic macrofaunal species of economic and ecological significance. The extensive *Sargassum siliquastrum* beds examined in the present study clearly

indicated the close association of subtropical seaweed beds with the zooplankton and epiphytic faunal assemblages. Management strategies for the protection of these seaweed beds should thus be part of any coastal developmental plan in order to ensure that this complex association is sustained for the future.

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